

THE STRATIGRAPHY AND AMMONITE FAUNA
OF THE UPPER LIASSIC GREY SHALES OF
THE YORKSHIRE COAST

BY
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SYNOPSIS

The Grey Shales is the lowest formation of the Upper Lias in Yorkshire, and is the type section of most of the *Tenuicostatum* Zone, the lowest zone of the Toarcian. The formation, consisting of 13.5 m of grey shale containing 15 rows of calcareous nodules, is described in detail, and there are geological maps of the two main outcrops. The Hildoceratid ammonite *Protogrammoceras paltum* (Buckman) occurs near the base of the formation, and a rich fauna of Dactylioceratidae occurs in the upper 10 m, which has been divided into four species of *Dactylioceras (Orthodactylites)*, including the new species *D. (O.) clevelandicum*. These ammonites form the basis of the following newly-proposed scheme of subzones:

| | | |
|--------------------|---|--|
| Tenuicostatum Zone | { | Subzone of <i>Dactylioceras (O.) semicelatum</i> |
| | | Subzone of <i>D. (O.) tenuicostatum</i> |
| | | Subzone of <i>D. (O.) clevelandicum</i> |
| | | Subzone of <i>Protogrammoceras paltum</i> |

A single example of *D. (Dactylioceras) pseudocommune* Fucini found in north-west Cleveland is also described, and is the earliest Dactylioceratid known in Britain. Correlations are made with all other areas of the world from which beds containing Tenuicostatum Zone ammonites have been described.

The preservation of the Grey Shales species of *Dactylioceras*, with the shell intact or as internal moulds, is complicated by the unique shell structure of Dactylioceratidae, in which a complete inner shell is formed. Four basically different appearances of the ribbing of the Yorkshire species are described.

I. INTRODUCTION

DETAILED descriptions of the stratigraphy and ammonite fauna of most of the Middle and Upper Lias of the Yorkshire coast have appeared in recent years. Only the Grey Shale "Series" (here called the Grey Shales) remains undescribed. It is the basal lithological division of the Upper Lias, overlying the Middle Lias Ironstone "Series" (Howarth 1955), and is overlain by the Jet Rock and Alum Shale "Series" (Howarth 1962), and then by higher beds at Ravenscar up to the top of the Lias (Dean 1954). With this description of the Grey Shales, the full succession is now complete from the base of the Middle Lias up to the top of the Upper Lias. The Yorkshire coast is the type area for many of the zones and subzones of the Middle and Upper Lias, and the Grey Shales make up most of the thickness of the *Tenuicostatum* Zone, the basal zone of the Toarcian or Upper Lias. It is the type area of both the *Tenuicostatum* Zone and the Toarcian Stage. The rich *Dacylioceratidae* ammonite fauna of the Grey Shales has enabled the *Tenuicostatum* Zone to be divided into subzones for the first time, on the basis of a thick, expanded succession. The discovery at the top of the Grey Shales of a rich *Tiltoniceras* fauna, previously known only from the Transition Bed of the English Midlands, shows for the first time that this ammonite occurs at the top of the *Tenuicostatum* Zone.

There is no satisfactory previous account of the stratigraphical succession within the Grey Shales of Yorkshire. Tate & Blake's (1876 : 168-172) general description of the lithology and occurrence of fossils is good, but neither of their two detailed sections is an adequate description of the constant succession of shales and doggers that occurs in the coastal exposures. No further description or details of the succession were given by Fox-Strangways & Barrow (1915 : 16) or by Buckman (1915a : 76) in the same work. A collection of 42 ammonites from the Grey Shales was made by Dr L. R. Cox in 1929, together with a bed by bed succession that can be identified with the sequence described here, and these ammonites are included in this description. Some work on the Grey Shales was done by Professor Sylvester-Bradley in the mid-1950s but has never been published. The bed numbers 1-32 were given by him in a manuscript account of the stratigraphical succession, and it was because of this account, which he kindly communicated to me, that the Cannon Ball Doggers immediately overlying the Grey Shales were given the bed number 33 (Howarth 1962 : 388). The only previous allusion to the stratigraphical sequence within the *Tenuicostatum* Zone was the four horizons listed by Dean, Donovan & Howarth (1961 : 476), also taken from Professor Sylvester-Bradley's manuscript account.

All the Grey Shales localities on the coast are foreshore reefs, and as the beds are less resistant than most other parts of the Middle and Upper Lias, they form some of the lowest reefs occurring almost wholly between "mid-tide" and low water mark. The reefs are flat wave-cut platforms sloping seawards at a very low angle, and the amount exposed differs greatly according to the type of tide. For this reason all the localities were visited at low water of spring tides. Geological maps were drawn for each locality on a scale of 1 : 2,500, the base maps used being the 1928 edition of the Ordnance Survey (the latest available), and on those reproduced here as Text-figs. 2 and 3 the lines drawn as "low water mark" are those of fairly

low spring tides. Considerably less is seen at low water of ordinary tides, and at neap tides exposures are even more restricted. Help in the correct alignment of the faults and some key beds shown on both maps was obtained from aerial photographs taken by Dr J. K. St. Joseph of Cambridge University, to whom thanks are due.

Most of the localities showing exposures of Grey Shales on the north-western escarpment of the Cleveland Hills between Saltburn and Osmotherley were also visited, mainly in order to examine the lowest beds. The succession was found to be no different from that on the coast, and it is only in the top few beds of the Ironstone "Series" that a different development occurs, with one of the beds containing a highly significant specimen of *Dactylioceras*.

II. STRATIGRAPHICAL SUCCESSION

The Grey Shales consists of 13.56 m (44 ft 6 in.) of grey shale, containing 15 rows of nodules or doggers of calcareous, and sometimes sideritic, argillaceous limestone. Pyritization occurs in some doggers and there are granular masses of pyrite in the upper shale beds. The doggers are distinctive and constant in all the exposures, and some of the rows form striking features. Thus bed 3 is a continuous bed of sideritic calcified mudstone which weathers red in patches, the Six Red Nodule beds (beds 7-17) occur as closely spaced rows of dark red nodules on many of the reefs, and beds 28 and 30 form long lines of frequent doggers prominent at all localities. Ammonites are abundant in the upper 9.80 m (32 ft) of the Grey Shales, and a collection of 560 well-preserved Dactylioceratidae was obtained from the nodules of beds 18, 19, 20, 22, 24, 28 and 30. A further 450 ammonites, mainly *Tiltoniceras*, were obtained from the shell beds in bed 32. The lower 3.76 m (12 ft 6 in.) contain very few ammonites, in fact only rare specimens have been found in beds 2 and 3, and there are none at all in beds 1 and 4-17. Belemnites are common at almost all horizons in the Grey Shales, including those that do not contain ammonites. Other faunal elements are much less common, and the bivalves and gastropods in the long list given by Tate & Blake (1876: 172) are only rarely found at most horizons. An exception is "*Posidonia*" *radiata* (Goldfuss), and perhaps other related species, which is abundant in shell beds in bed 32 and common at other horizons.

The upper limit of the Grey Shales and also of the Tenuicostatum Zone is now placed at the top of bed 32 and not at the bottom of bed 32 as previously (Howarth 1962: 388), following the discovery of many crushed *Dactylioceras semicelatum* throughout that bed. It was also realized that the commonest ammonite in bed 32, especially in two shell beds at the base, is *Tiltoniceras antiquum* (Wright) and not *Eleganticeras elegantulum* (Young & Bird) as recorded previously (Howarth 1962: 388). Both *Dactylioceras semicelatum* and *Tiltoniceras* are traditionally ammonites of the Tenuicostatum Zone, and so the top boundary of the zone has to be placed at the top of bed 32. The top of the Grey Shales is placed at the same position because the shales of bed 32 are similar to those of the beds below, and real bituminous shales start in bed 34 immediately above the Cannon Ball Doggers at the base of the Jet Rock.

The lower limit of the Grey Shales is at the base of bed 1, immediately above the top bed of the Ironstone "Series" (Kettleness bed 28). The position of the base of the *Tenuicostatum* Zone is a complicated question involving lithological and palaeontological correlations and is fully discussed later (p. 267).

The following detailed succession is constant for all the localities at which the Grey Shales are exposed, for the lithology shows no variation and the thickness shows very little variation. The thicknesses were, in fact, measured in vertical cliff sections as follows: beds 1-18 at Brackenberry Wyke, Runswick Bay, west and east Kettleness, and Hawsker Bottoms; beds 18-32 at east Kettleness; beds 22-32 at Loop Wyke and Hawsker Bottoms; and beds 28-32 at Brackenberry Wyke. The beds of nodules are of constant thickness, while shale beds may vary by up to 25% between thickest and thinnest, but usually the variation is considerably less. Fossil records are included from all the exposures, numbers prefixed by "C." being the register numbers of specimens in the collections of the British Museum (Natural History), while the first prefix letter *a* to *k* indicates the locality from which the specimen came as listed on pp. 242-244.

| Bed no. | | m | (ft in.) |
|---------|---|------|----------|
| 33 | The Cannon Ball Doggers. Basal bed of the JET ROCK, Exaratum Subzone. <i>Eleganticeras elegantulum</i> (Young & Bird) | 0.15 | (0 6) |
| | Zone of <i>Dactylioceras tenuicostatum</i> | | |
| | Subzone of <i>Dactylioceras semicelatum</i> | | |
| | THE GREY SHALES. Total thickness 13.56 m (44 ft 6 in.) | | |
| 32 | Shale, grey, bituminous in places, with occasional flat calcareous nodules near top, constant and widespread shell-beds at base and 0.10 m above base, and occasional shell-beds throughout. Basal two shell-beds contain large numbers of crushed <i>Tiltoniceras antiquum</i> (b C.50407-12, C.77349-59; f C.77364; h C.77361-63), <i>Dactylioceras semicelatum</i> (b C.47941, C.77360; f C.77365; g C.77366) and " <i>Posidonia</i> " <i>radiata</i> (Goldfuss). The same species occur less abundantly in shell-beds up to 0.30 m below top— <i>T. antiquum</i> (h C.77369), <i>D. semicelatum</i> (j C.77367, 68; k C.77369-74) | 1.83 | (6 0) |
| 31 | Shale, grey. Crushed <i>Dactylioceras semicelatum</i> throughout, some in shell-beds, but especially common near middle of bed (b C.77343, 44; c C.47932; f C.77341, 42; g C.77340; j C.77345-48) | 2.13 | (7 0) |
| 30 | Large, very hard, calcareous doggers, with much pyritization, average size 0.15 m × 0.20 m × 0.10 m thick. <i>Dactylioceras semicelatum</i> common, usually horizontal through middle of doggers, occasionally at varying angles (b C.47955, 56, C.77318-26; c C.47931, 33, 34, C.77327, 28; f C.77297-314; g C.77315, 16; h C.77329-32; j C.77333-39; k C.77317) | 0.10 | (0 4) |
| 29 | Shale, grey, granular pyrites common, especially in lower half. Occasional crushed <i>Dactylioceras semicelatum</i> | 1.07 | (3 6) |
| 28 | Large, hard, calcareous doggers, in two adjacent rows; less pyrite than in doggers of bed 30, and individual doggers rather smaller, average size 0.12 m × 0.15 m × 0.08 m thick, but upper row larger than lower row. Knots of pyrites in shale between doggers. <i>Dactylioceras semicelatum</i> in some doggers (b C.47940, 46, 53, 54, | | |

| Bed no. | | m | (ft in.) |
|---|--|------|----------|
| | C.77276-78, C.77283, 84; c C.47936, 38, 39, 57, C.77269; f C.77270-75; h C.77285-94; k C.77279-82), large belemnites in others, also <i>Cenoceras astacoides</i> (Young & Bird) (b C.50414) | 0.23 | (0 9) |
| Subzone of <i>Dactylioceras tenuicostatum</i> | | | |
| 27 | Shale, grey. Rare crushed specimens of <i>Dactylioceras tenuicostatum</i> . | 0.61 | (2 0) |
| 26 | Thin calcareous nodules, flat and lens-shaped, weathering red. A few <i>Dactylioceras tenuicostatum</i> (f C.77257, 58; g C.77263-66; h C.77267, 68; k C.77259-61) | 0.05 | (0 2) |
| 25 | Shale, grey with occasional round calcareous nodules containing <i>Dactylioceras tenuicostatum</i> | 0.61 | (2 0) |
| 24 | Row of small spherical calcareous nodules, almost all with one <i>Dactylioceras tenuicostatum</i> lying horizontally through the middle (b C.47947, C.77225-56; d C.47923; f C.47926, 27, C.77187-215; h C.77220-24; k C.77216-19) | 0.08 | (0 3) |
| 23 | Shale, grey, occasional round calcareous nodules containing <i>Dactylioceras tenuicostatum</i> | 0.38 | (1 3) |
| 22 | Row of nodules as bed 24. <i>Dactylioceras tenuicostatum</i> (b C.47951, 52, C.77178-86; c C.47937, C.77159-69; d C.47912, 14-19, 24, 25; f C.77148-58; g C.50413, C.77170; h 77173-77; k C.77171, 72) | 0.08 | (0 3) |
| 21 | Shale, grey, occasional small calcareous nodules with <i>Dactylioceras tenuicostatum</i> (d C.47920-22) | 0.76 | (2 6) |
| 20 | Large scattered calcified lenses, weathering red; each lens about 0.25 m across and 0.07 m thick, and occurring in two adjacent rows. <i>Dactylioceras tenuicostatum</i> (b C.77120-47; f C.77110-19; g C.77109) | 0.15 | (0 6) |
| Subzone of <i>Dactylioceras clevelandicum</i> | | | |
| 19 | Shale, subdivided as follows: | | |
| 19c | Shale, grey | 0.81 | (2 8) |
| 19b | Shale, grey, with scattered thin, flat, lens-shaped concretions, weathering red. Calcified clusters of <i>Dactylioceras clevelandicum</i> lying at all angles occur commonly between the red concretions (a C.50415-18, C.77077-84; b C.47944, 45, 48, C.76988, 89, C.77094-108; c C.77085-88; d C.77052-76; e C.77093; f C.76925-87; g C.50419-26, C.76990-77051; h C.77089-92) | 0.05 | (0 2) |
| 19a | Shale, grey, basal 0.10 m closely laminated and bituminous, and weathers to form a step on foreshore reefs; pale brown sandy masses 0.30 m above the base | 0.41 | (1 4) |
| 18 | Shale, grey, silty; small calcareous nodules or calcified clusters of <i>Dactylioceras crosbeyi</i> lying at all angles occur in a row at the middle of the bed (b C.47950, C.76917-19; c C.76920; d C.47913, 42, 43; e C.76913-16; f C.76860-90; g C.76891-912; h C.76921-24) | 0.38 | (1 3) |
| Subzone of <i>Protogrammoceras paltum</i> | | | |
| 17 | Sixth Red Nodules. Row of frequent grey calcareous and sideritic nodules, weathering deep red on the outside, average size 0.23 m x 0.15 m x 0.05-0.08 m thick. Some contain large belemnites and more rarely bivalves. No ammonites | 0.08 | (0 3) |
| 16 | Shale, grey | 0.20 | (0 8) |
| 15 | Fifth Red Nodules. As bed 17 | 0.08 | (0 3) |
| 14 | Shale, grey | 0.23 | (0 9) |
| 13 | Fourth Red Nodules. As bed 17 | 0.05 | (0 2) |

| Bed no. | | m | (ft in.) |
|---|--|------|----------|
| 12 | Shale, grey | 0.30 | (1 0) |
| 11 | Third Red Nodules. As bed 17 | 0.05 | (0 2) |
| 10 | Shale, grey | 0.25 | (0 10) |
| 9 | Second Red Nodules. As bed 17 | 0.05 | (0 2) |
| 8 | Shale, grey | 0.41 | (1 4) |
| 7 | First Red Nodules. As bed 17 | 0.08 | (0 3) |
| 6 | Shale, grey | 0.53 | (1 9) |
| 5 | Row of small, spherical, grey calcareous nodules. No ammonites | 0.05 | (0 2) |
| 4 | Shale, grey | 0.36 | (1 2) |
| 3 | Continuous bed of sideritic, calcareous mudstone, weathering red. Rare large specimens of <i>Protogrammoceras paltum</i> (d C.47972; f C.77296; k C.72521, C.77262), and crushed <i>Dactylioceras</i> sp. indet. (f. C.77295) | 0.08 | (0 3) |
| 2 | Shale, dark grey, closely laminated and bituminous; marked parting 0.20 m below top at some localities. Small calcareous nodule at base with impression of a <i>Lytoceras</i> sp. indet. (locality f) | 0.53 | (1 9) |
| 1 | Shale, grey | 0.51 | (1 8) |
| THE IRONSTONE SERIES (see Howarth 1955 : 156—bed numbers of Kettleness section) | | | |
| 28 | Row of frequent round calcareous nodules. Many <i>Pseudopecten aequivalvis</i> (J. Sowerby), and <i>Pholadomya ambigua</i> (J. Sowerby) in vertical life position | 0.05 | (0 2) |
| 27 | Shale, sandy | 0.46 | (1 6) |
| 26 | Shale, closely bedded, bituminous (= Sulphur Band) | 0.15 | (0 6) |
| Zone of <i>Pleuroceras spinatum</i> | | | |
| Subzone of <i>Pleuroceras hawskerense</i> | | | |
| 25 | Shale, grey, sandy. Limestone nodules near base contain many <i>Pleuroceras hawskerense</i> (Young & Bird) | 0.33 | (1 1) |

DETAILS OF LOCALITIES (Text-fig. 1)

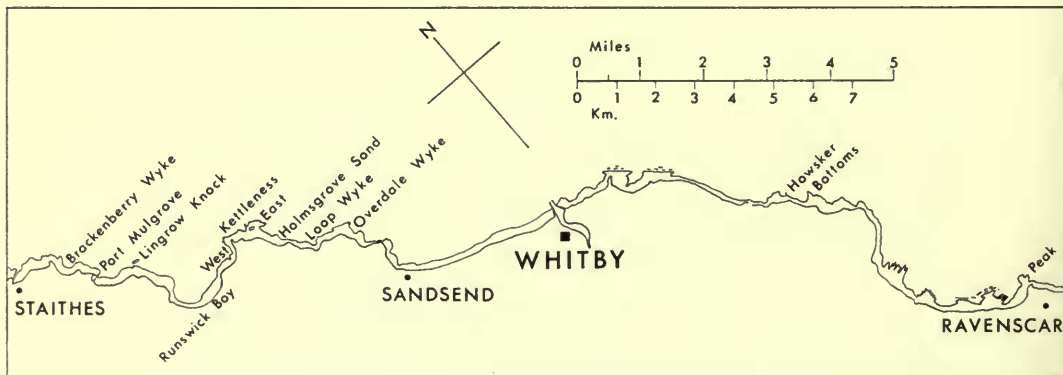


FIG. 1. Localities of exposures of Grey Shales on the foreshore of the north Yorkshire coast.

a. Brackenberry Wyke (see Text-fig. 2). The base of the Grey Shales first appears on the foreshore in Brackenberry Wyke at NZ 795185. Beds 3 and 5 follow, then

the Six Red Nodule beds form a striking feature running approximately north-south at NZ 796182. Beds 18 and 19 appear, but large boulders cover much of the upper half of bed 19 and bed 20. All the beds dip at a low angle to the east.

b. Port Mulgrave (see Text-fig. 2). The last exposure continues south-eastwards across Thorndale Shaft now clear of boulders, and all the beds are seen up to the top of the Grey Shales. A north-south double fault crosses the reef at NZ 799179, and with an upthrow of about 5 m (16.5 ft) to the east, most of the Grey Shales are repeated again on the eastern side of the fault. The lowest bed seen at low water of spring tides is the First Red Nodules, bed 7, then higher beds follow southwards up to beds 30 and 31 which abut the north pier of Port Mulgrave (NZ 800177). Immediately south of the south pier beds 19-32 appear again on foreshore reefs, and beds 31 and 32 occupy the seaward half of the reef across the whole of Rosedale Wyke eastwards to Lingrow Knock (see Howarth 1962 : pl. 26).

The whole of the outcrop starting in Brackenberry Wyke and ending in Rosedale Wyke is well exposed and forms a good collecting ground.

c. Lingrow Knock. The Runswick Bay Fault, consisting here of two parallel north-south faults about 8 m apart, crosses the reefs immediately west of Lingrow Knock (NZ 809173), and throws the beds up to the east by about 14 m (45 ft) (Howarth 1962 : pl. 26). The whole of the Grey Shales occupies the reef east of the fault, the strike of the beds now being east-west with a slight dip to the south. The lowest beds occur at low water mark and the highest at the base of the cliff, but beds 5-7 are missing, cut out by a small fault. The detached reef of Lingrow Knock (which is easily accessible at low spring tides) consists largely of the top ironstone of the Ironstone Series (Kettleness bed 24, Howarth 1955 : 156). The nodules of bed 28 and then the base of the Grey Shales occur farther south on the seaward edge of the main reef. This exposure is covered by boulders at its south-eastern end.

d. Runswick Bay. Apart from a small exposure of beds 31 and 32 at the north end of Topman Steel (NZ 811168) north of Runswick, the next exposure of Grey Shales is the large reef occupying the south-eastern half of Runswick Bay. The strike is north-south and the dip to the west. The ironstone of Kettleness bed 24 occupies the eastern half of the reef, the base of the Grey Shales crosses the reef north-south at NZ 820155, then higher beds follow westwards up to bed 33 seen at the extreme western tip of the reef at NZ 815156. The Six Red Nodule beds and parts of beds 19 and 20 are well seen, but the remainder of the exposure is not good for collecting, being wet and largely covered with seaweed.

e. West Kettleness. The whole of the Grey Shales occurs on a small reef on the west side of Kettleness at NZ 829159. The beds strike north-south and dip at a low angle to the west, so the base is at the eastern end and the top at the western end of the reef. The lower half and the top beds are well seen, but beds 22 and 24 are difficult to trace.

f. East Kettleness (see Text-fig. 3). This large and structurally complicated exposure starts at NZ 836160, surrounds the hole in the reef known as Fillet Tail Dump, and extends to about NZ 839158 where boulders cover all but the seaward edge. The structure is a syncline dipping to the south at a low angle, so the base of the Grey Shales forms a semicircle round the west, north and east sides, and the top is at the base of the cliff to the south. Six or seven minor faults break up the semicircular continuity of the beds (Text-fig. 3). This is one of the best collecting localities for all horizons of the Grey Shales, which are very well exposed on the southern half, but wet and seaweed covered north and east of Fillet Tail Dump.

g. Holmsgrove Sand (see Text-fig. 3). The last exposure continues south-eastwards, now clear of boulders, to the cliff behind Holmsgrove Sand, until the foreshore is covered by a major cliff slump at NZ 842153. A north-west to south-east striking thrust fault cuts the reef into two parts, but all beds of the Grey Shales are exposed down to the two top beds of the Ironstone Series (beds 27 and 28) at NZ 842154. One of the best collections from bed 19*b* was made at this locality.

h. Loop Wyke. Small isolated reefs with beds 23–31 occur on the north side at NZ 845149. The main reef at NZ 848147 exposes beds from the middle of bed 21 (at low water of spring tides) up to the Jet Rock, and good collections were obtained from beds 28 and 30.

j. Overdale Wyke. Bed 33 runs east-west through the middle of Keldhowe Steel at NZ 855147, the top of the Grey Shales occurs to the south, and beds 29–31 occupy the whole of the reef in Overdale Wyke southwards as far as NZ 858142. The nodules of bed 30 form a large arcuate outcrop on the reef. Small outcrops of beds 31 and 32 occur under the cliff in Deepgrove Wyke at NZ 858140.

k. Hawsker Bottoms. The lower boundary of the Grey Shales occurs on the west of Hawsker High Scar at NZ 951077. The dip is at a low angle to the west, and higher beds follow westwards up to the base of the Jet Rock at NZ 948078. The basal beds, the Six Red Nodule beds and beds 28–32 are well exposed, but beds 20–27 are largely obscured and difficult to trace beneath boulders. The top bed of the Ironstone Series, bed 28 (bed 44 of Howarth, 1955 : 154) is rather different at this locality, being a near-continuous bed of red-weathering nodular limestone.

l. Peak, Ravenscar. Immediately east of the Peak Fault at NZ 980027 there is a small exposure of part of the Grey Shales (Howarth 1962 : pl. 27). The top beds of the Ironstone Series and beds 1–11 of the Grey Shales occur near low tide mark, and beds 28–32 occur to the south below the exposure of Jet Rock described previously (Howarth 1962 : 393–395). Beds 12–27 are entirely obscured by boulders. Although it is a small exposure, beds 3 and 5, the lowest three of the Six Red Nodule beds, and the doggers of beds 28 and 30 are well seen, and they do not differ in lithology or thickness from the standard Grey Shales succession on the western side of the Peak Fault. Thus the different lithology found in some higher beds of the Upper Lias on this eastern side of the Peak Fault does not apply to the Grey Shales.

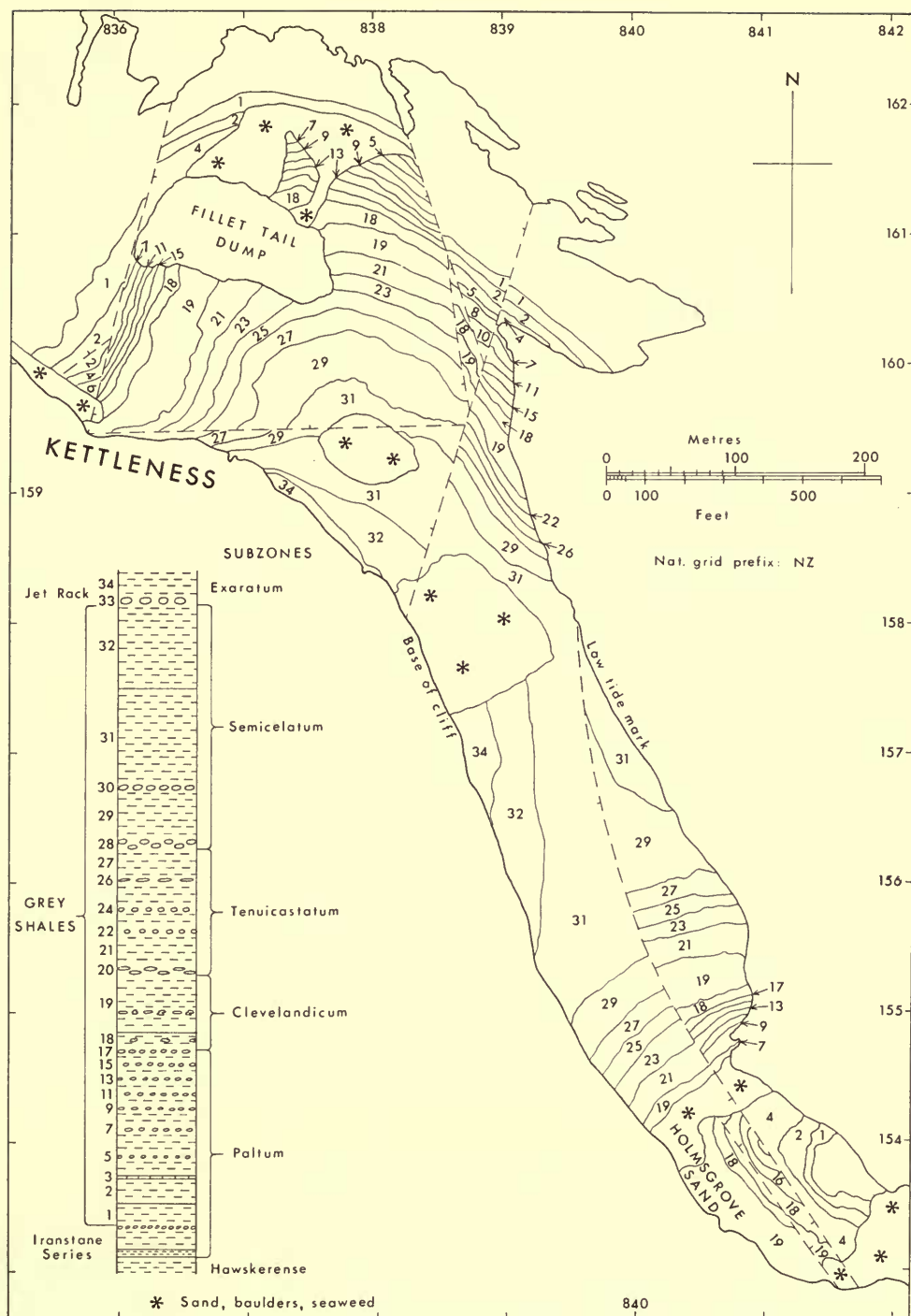


FIG. 3. Geological map of the Grey Shales on the foreshore at Kettleiness.

THE SUCCESSION IN NORTH-WEST CLEVELAND

In marked contrast to the constant Upper Liassic Grey Shales, the Middle Liassic Ironstone Series shows so much lateral variation in thickness and facies that three different successions had to be described for the coastal exposures (Howarth 1955). Later, the development of the Ironstone Series in the Eston area of north-west Cleveland was described by Chowns (1966). Many details of the variable succession were given by Tate & Blake (1876: 119-152). In that area there is a disconformity at the top of the Main Seam Ironstone, and the overlying "Sulphur Band", an argillaceous bed full of oolite grains and much pyrites about 0.10 m thick, is correlated with Kettleness bed 26 (Howarth 1955: 156, = Staithes bed 58). Above the "Sulphur Band" comes the Top Main Dogger, an oolitic ironstone up to 1.00 m thick similar to the Main Seam Ironstone. This is the top of the Ironstone Series and is overlain by the Grey Shales. All the exposures of these beds in the north-west scarp of the Cleveland Hills between Skelton and Osmotherley were visited to examine these horizons. The only place where a satisfactory exposure of the bottom of the Grey Shales could be seen was in a cliff at the side of a stream at Hutton Lowcross (NZ 604134). The Six Red Nodule beds were definitely located, and a thickness of 2.56 m (8 ft 5 in.) of shales was measured below them down to the top of the Top Main Dogger. There is a bed of nodules, possibly Grey Shales bed 5, 0.81 m (2 ft 10 in.) below the top of the shales. It is concluded that the Grey Shales are probably complete down to the bottom of bed 1, and that the Top Main Dogger is the lateral equivalent of Kettleness beds 27 and 28, the top two beds of the Ironstone Series.

This lithological correlation is important because a single specimen of *Dactylioceras pseudocommune* Fucini found in an old ironstone mine at Hob Hill (NZ 653203), near Saltburn, is much the oldest *Dactylioceras* in the English Lias. Its exact horizon was not recorded, but the matrix is a pale green ironstone with white ooliths like both the Main Seam Ironstone and the Top Main Dogger. If it is from the Main Seam its age has to be Apyrenum Subzone, the lower half of the Spinatum Zone, and this would make it the earliest known *Dactylioceras* from anywhere. If from the Top Main Dogger, on the other hand, it would be above the highest *Pleuroceras* and would be taken as indicating the base of the Tenuicostatum Zone. This is compatible with the basal Tenuicostatum Zone age of the earliest *Dactylioceras* in the Mediterranean area, and so it is considered much more likely that the Hob Hill specimen came from the Top Main Dogger than from the Main Seam Ironstone. The lower boundary of the Tenuicostatum Zone is placed, as explained on p. 267, at the base of the Sulphur Band below the Top Main Dogger.

III. PALAEOLOGY

Family DACTYLIOCERATIDAE Hyatt, 1867

The classification of ammonites of this family poses problems totally different from those of the contemporaneous Hildoceratidae. Ammonites of both families present a bewildering range of morphology until stratigraphical relationships are known. Collections of Hildoceratidae from single horizons show that species are

relatively closely defined, and the phenomenon of dimorphism is immediately apparent in many cases. In marked contrast, single bed collections of Dactylioceratidae sometimes present a very large range of continuously variable morphology, and a convincing case of dimorphism has yet to be found. The Dactylioceratidae of the Yorkshire coast Grey Shales have been collected with a degree of stratigraphical control upon which it would hardly be possible to improve. This is because they occur abundantly in nodules or calcified clusters at seven main horizons (i.e. beds 18, 19b, 20, 22, 24, 28 and 30), in a sequence that is clearly not condensed, and where each bed of nodules is at a constant horizon (except bed 28). Collections from these beds do not represent single populations in a biological sense, but they do represent single populations in the sense that it is almost certain that no evolution has occurred within the collection from each bed. Each such collection consists of ammonites that exhibit a very large amount of variation in some of the whorl proportions, in rib density, and in the size of the ventro-lateral tubercles. The greatest variation occurs in whorls of between about 50% and 75% of the average adult size: for example in bed 30 whorl height varies between 16 and 23 mm, and umbilical width between 33 and 44 mm, both at 72 mm diameter, while whorl breadth varies very widely between 11 and 24 mm at 50 mm diameter, and the number of ribs per whorl varies between 31 and 85 at the same diameter. Graphs plotted of whorl proportions and rib-density against diameter show that the variation is continuous in each collection, and confirm the impression that there are no morphological breaks in the variation. Whorl breadth and rib-density are inter-related to some extent, for it is specimens with compressed whorls that are more densely ribbed, and those with depressed whorls that are more sparsely ribbed, though the variation in rib-density is still considerable in specimens with similar whorl breadths. There are no specimens with depressed whorls in beds 22 and 24, the variation in whorl breadth being less than one-third of the variation in beds 18, 19, 28 and 30, yet the variation in rib-density in beds 22 and 24 is just as great as at any of the other horizons.

The variation is much less on the final adult whorl, so that all the depressed, tuberculate specimens have more compressed adult body chambers. The specimen figured in Pl. 4, fig. 2 is one of the best examples of highly depressed and strongly tuberculate inner and middle whorls that become completely different on the final adult whorl, which is much more like the specimens with compressed whorls from the same bed. Other such examples are shown on Pl. 1, fig. 3, Pl. 3, fig. 2 and Pl. 9, fig. 1. Specimens showing the full range of morphological variation at each horizon are figured in the plates, and Text-figs. 5 and 6 are graphical representations of the amount of variation.

In erecting a classification for these Grey Shales Dactylioceratidae a choice has to be made between referring all the specimens from one horizon to a single variable species, or dividing up the morphological variation into different species and genera. The amount of variation at each horizon is sufficient to divide the collections into two genera (one compressed, one depressed) and up to four species, according to the scale of differences traditionally adopted by palaeontologists for Dactylioceratidae. The genus *Dactylioceras* (*Orthodactylites*) would be used for the compressed groups,

and the name *Kedonoceras* Dagis is available for the depressed groups. The conclusion to be drawn from such a classification is that the three different species of *Kedonoceras* that would be required at different horizons were more closely related to each other than they were to the species of *Dactylioceras* (*Orthodactylites*) that each of them accompanied. Yet the variation at each horizon appears to be continuous between the end forms, so the splitting into species and genera would be by means of arbitrary morphological divisions; moreover, the adult body chambers of all the species of "*Kedonoceras*" revert to a morphology much closer to the accompanying compressed species, so that the term *Kedonoceras* would really have only been applied to the inner and middle whorls.

These considerations have led to the belief that it is better, and probably phylogenetically more correct, to refer all the specimens at each horizon to a single variable species of *Dactylioceras* (*Orthodactylites*). The form of the adults and the continuity of the variation seem to indicate that the depressed forms are more closely related to the compressed forms at the same horizon than they are to the depressed forms at other horizons. Examination and analysis of the whole collection has led to the recognition of four successive species: one in bed 18, one in bed 19b, one in beds 20, 22, 24 and 26 which shows minor sub-specific evolutionary trends, and finally one in beds 28 and 30-32. These four species are largely distinct from one another in all their forms, and only in the case of the highest and the lowest species are some of the forms sufficiently alike to make separation difficult. Three of the four subzones erected in this paper are based on the stratigraphical succession of these four species. Division of the collection in a different way according to traditional morphology would not make any difference to the stratigraphical results.

Taxonomy according to these methods and stratigraphical control leads to an entirely different classification from that obtained by means of orthodox morphological taxonomy. Thus, in a recent work, Pinna & Levi-Setti (1971) erected a morphological classification for Mediterranean Dactylioceratidae that had little accurate stratigraphical control. The oversplitting that resulted and the separation of closely similar forms (e.g. *Nodicoeloceras* and *Mesodactylites*) would probably break down if stratigraphical associations were known. One such association which is accurately known is that of *Porpoceras* in Yorkshire: the fauna occurs only in beds xlii and xliii of the Braunianus Subzone at Ravenscar (Howarth 1962: 400), and specimens show a wide range of variation in whorl breadth that is the basis of the three specific names *P. vortex* (Simpson), *P. verticosum* Buckman and *P. vorticellum* (Simpson). The variation is continuous and the whole fauna is linked together by features of the ribbing that are characteristic of *Porpoceras*. According to the taxonomy adopted here the whole fauna would be referred to the single species *P. vortex*; even if the three species were upheld, they would have to be referred to *Porpoceras*; but Pinna & Levi-Setti (1971: 107, 121) placed *P. verticosum* and *P. vorticellum* in *Nodicoeloceras* (a genus said to belong to the Mediterranean subfamily "Mesodactylioceratinae") and *P. vortex* in *Peronoceras* (a genus of the north-west European "Dactylioceratinae"). Faunal associations like *Porpoceras* are the basic units on which a classification should be built, and any classification which splits them up into different genera said to belong to different provinces must fail.

The north-east Siberian genus *Kedonoceras* Dagis (1968) probably consists of the depressed variants of Tenuicostatum Zone *Dactylioceras* (*Orthodactylites*), some of them possibly conspecific with those in the Yorkshire Grey Shales. As in Yorkshire they occur below faunas of *Tiltoniceras*. All the known specimens are small (up to 53 mm diameter), and in the absence of any adults it is not possible to be certain where they belong. The subfamily name Kedonoceratinae proposed for them, and to include also the totally unrelated Bifrons and Variabilis Zone genera *Porpoceras*, *Collina* and *Catacoeloceras*, cannot be accepted as a grouping for these mainly depressed forms, that have a suture-line shape dependent of the shape of the whorl. The depressed forms known as *Kedonoceras* are more closely related to the *Dactylioceras* (*Orthodactylites*) that they accompany than they are to any other depressed Dactylioceratidae. The placing of *Kedonoceras* in the synonymy of *Porpoceras* by Guex (1971: 231) is another example of how a classification based mainly on morphology can bring together two forms that are widely separated stratigraphically and not related in any way.

The Grey Shales Dactylioceratidae show no evidence of dimorphism. A considerable number of adult specimens are known (more than 100 were examined) and in each species the size range of adults forms a single group with an even distribution between largest and smallest. The ratio of largest to smallest adults in the four species recognized is 1.55, 1.67, 1.46 and 1.60. These figures are considerably less than the ratios of 2.0 to 3.0 that have been found for each dimorph of several dimorphic species of Hildoceratidae. There is no other evidence for dimorphism in the Grey Shales species. Dimorphism in Dactylioceratidae was first claimed by Lehmann (1968) for two species: in *D. ernsti* one dimorph was said to be 55–60 mm diameter, the other 90 mm, there being no other differences, a distinction that is not considered here to be sufficient to claim dimorphism; in *D. athleticum* one dimorph was said to be 40–47 mm diameter, the other 67–93 mm, and there are apparently consistent differences in the spacing of the first 12 septae. Again the evidence is not thought sufficient to uphold it as a case of dimorphism. The recognition of dimorphism throughout the Dactylioceratidae has been claimed by Guex (1971), but the number of known specimens that could be microconchs is very small. Most of them could be abnormal or could be specifically different from the macroconchs that they are said to accompany. The evidence for dimorphism is summed up in the Yorkshire occurrences: Hildoceratidae and Dactylioceratidae existed together during much of the Upper Lias; the Hildoceratidae show abundant evidence of dimorphism, the Dactylioceratidae show none.

Shell structure and preservation

The appearance of the Grey Shales Dactylioceratidae is greatly influenced by the unique shell structure of ammonites of that family. Many cases are known of the deposition of various shell structures within the body chambers of ammonites, such as the floor cutting off an originally hollow keel, septae at the base of long spines or tubercles, and a dorsal shell (or callus) laid down on top of the ventral part of the

shell of the previous whorl to fill in irregularities of the ornament. But a continuous inner shell lining the whole of the lateral and ventral parts of the inside of the main shell has only been found so far in Dactylioceratidae, and was first described by Guex (1970). The point of formation of this inner shell is between one-eighth and one-quarter of a whorl behind the mouth border, and the front growing edge is angled forwards from the umbilical seam to the venter at about 45° to the radial line. The inner shell fills in the ornament of the main shell to a great extent, cutting off cavities inside the ribs which have characteristic flat floors, and the relief of the ribs on the inside of the inner shell is only a small fraction of the relief of the ribs of the main shell. The inner shell is continuous over the ventral and lateral parts of the main shell up to the umbilical seams, and is apparently absent or only partly formed on the dorsum between the umbilical seams. The absence of the inner shell on the dorsum is clearly seen on some very well-preserved Dactylioceratidae from west Northamptonshire, but one of the Grey Shales specimens (Text-fig. 4B) shows what is apparently dorsal infilling of some of the spaces between the ribs on the venter of the previous whorl, by means of layers of shell near the top of the intercostal spaces which cut off cavities below (CD on Text-fig. 4B). The position of commencement of the inner shell on the inner whorls is uncertain. The characteristic flat-topped ribs start $2\frac{1}{2}$ to $2\frac{3}{4}$ whorls before the adult mouth border in the Grey Shales specimens, and there is evidence that the inner shell occurs on at least one further inner whorl, but without forming cavities in the ribs of the main shell. So the inner shell starts on the 4th whorl before the adult aperture or earlier (complete specimens of *Dactylioceras* have approximately 7 whorls).

Polished sections of parts of several Grey Shales specimens were prepared to show the shell structure, and drawings made from two of them are shown in Text-fig. 4. Both are from near the middle of the venter; fig. 4A is from an adult body chamber, while fig. 4B is from a phragmocone rather more than one whorl before the mouth border, and shows parts of the siphuncle and the septa, which were laid down after the inner shell. The shell structure on the lateral parts of the whorl is similar, and in specimens with ventro-lateral spines the inner shell forms an arched floor at the base of each spine. In all the Grey Shales specimens the cavities in the ribs between the main and inner shells are filled with secondary calcite or occasionally with iron pyrites, but the cavities in well-preserved Northamptonshire Dactylioceratidae are empty.

The main shell consists of the three layers that are normally found in ammonites: a thin Outer Prismatic Layer, a thick Nacreous Layer and a thin Inner Prismatic Layer. So far as can be ascertained the inner shell consists of a fairly thick outer nacreous layer and a thin inner layer of prismatic crystals.

Grey Shales Dactylioceratidae have four basically different surface appearances according to the shell layer surface that is seen:

(1) The outer surface of the main shell is rarely seen, because most specimens are preserved inside nodules and there is strong adhesion between the main shell and the enclosing matrix. Occasionally this surface is seen on the last part of the body chamber near the mouth border when the main shell remains attached to the ammonite, but in most cases the shell breaks off with the enclosing matrix. When

seen, this shell surface has broadly rounded ribs with deep intercostal spaces of similar width to the ribs. Examples of this preservation are seen in Pl. 1, fig. 1, the final $\frac{1}{3}$ whorl of Pl. 1, fig. 4, Pl. 2, fig. 4, Pl. 8, fig. 4 and Pl. 9, fig. 3. Sometimes the main shell is preserved intact on the inner whorls, while missing on the outer two whorls. Thus on the inner whorls of Pl. 4, fig. 2 most of the main shell is preserved, with one or two of the spines nearly complete.

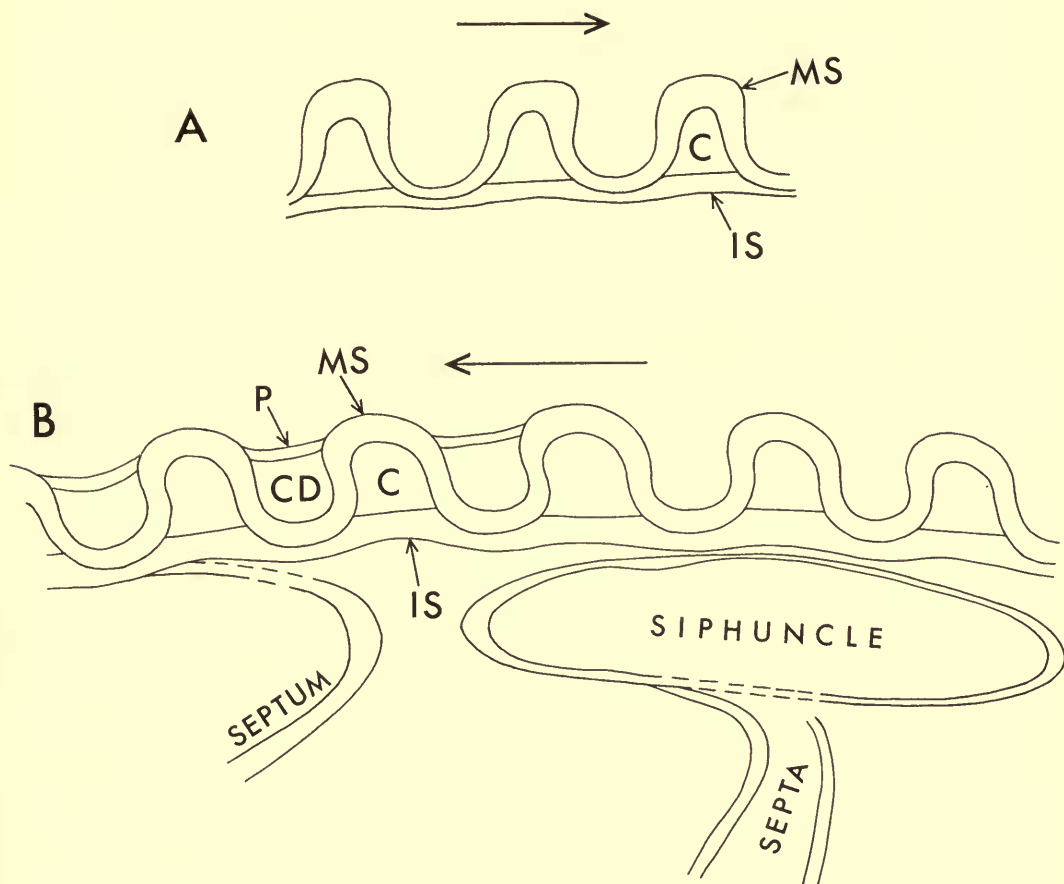


FIG. 4. Shell structure in two specimens of *Dactylioceras semicelatum* (Young & Bird). Sections through the shell showing: MS—the main (outer) shell. IS—the inner shell. C—the cavity between main and inner shells, now filled with secondary calcite or iron pyrites. P—partitions cutting off some of the intercostal spaces, laid down as dorsal shell of the next outer whorl. CD—the cavity between the main shell and the dorsal partitions of the next outer whorl, now filled with secondary calcite. Arrows indicate direction of the aperture. A—section near the middle of the venter of the adult body chamber, one-third of a whorl before the mouth border. C.77306, bed 30, east Kettleiness. $\times 11$. B—section at the middle of the venter of the phragmocone $1\frac{1}{8}$ whorls before the adult mouth border. An oblique section through the siphuncle and parts of three septa are seen. C.77317 (Pl. 9, fig. 1), bed 30, Hawsker Bottoms. $\times 11$.

(2) An internal mould of the inner surface of the main shell is seen near the apertures of most specimens that are complete to the mouth border, and when the shell breaks off with the enclosing matrix. The ribs are of high relief, but are noticeably thinner than in (1) above, and the intercostal spaces are much wider. Many of the complete adults figured in the plates show this type of preservation on the final part of the outer whorl: e.g. Pl. 2, fig. 2, Pl. 3, figs. 1, 2, Pl. 5, fig. 2 and Pl. 6, fig. 3, in all of which the ribs are of much higher relief on the final part of the whorl due to the absence of the inner shell.

A different occurrence of the preservation of the form of the inner surface of the main shell occurs when the inner shell is attached to the ammonite and calcite casts of the cavities between the two shells (C in Text-fig. 4) remain in place. The whole forms a perfect replica of the inside surface of the main shell, but is only occasionally found.

(3) The commonest type of preservation in the Grey Shales Dactylioceratidae is with the inner shell attached to the ammonite after the main shell has broken away with the enclosing matrix. The outer surface of the inner shell has characteristically flat-topped ribs of relatively low relief, and this is the type of ornament seen in most of the specimens that have shell attached which are figured in the plates. Good examples are Pl. 6, fig. 2, Pl. 7, figs. 1 and 2, and Pl. 8, figs. 1 and 2, in all of which the flat-topped ribs can be seen. In some specimens of *Dactylioceras semicelatum* from beds 28 and 30 the inner shell is replaced by iron pyrites in the phragmocone, so that a cast in pyrites of the outer surface of the inner shell is seen. This usually occurs in patches, and there are areas where the pyritic replacement merges into original shell. The specimen in Pl. 8, fig. 2 is preserved in this way, and approximately half the figured side is a pyritic cast of the inner shell. The whole of the phragmocone of Pl. 7, fig. 1 is similarly preserved, but in this case many intercostal parts of unaltered (i.e. calcitic) main shell remain attached to the pyrites-replaced inner shell. In a few places pyritic casts of the cavities between the main and inner shells are preserved. This pyrites-replaced inner shell overlies recrystallized calcite inside the phragmocone, and in a zone of partial replacement near the final septum the outer surface of the inner shell has a skin of pyrites. On the body chamber the inner shell is calcitic and overlies an internal mould of pyrites.

(4) When both the main and inner shells break off, the ammonite consists of an internal mould showing the ornament of the inner surface of the inner shell. The ribs and intercostal spaces are smoothly rounded and of much lower relief than either surface of the main shell. Most parts of the specimens figured in Pl. 1, fig. 2, Pl. 2, fig. 2, Pl. 3, figs. 1 and 2, Pl. 4, fig. 2 (outer whorl), Pl. 5, fig. 2 and Pl. 6, fig. 3 are preserved in this way.

Genus *DACTYLIOCERAS* Hyatt, 1867

TYPE SPECIES: *Ammonites communis* J. Sowerby, 1815, designated ICZN Opinion 576, 1959.

The general characters and long synonymy of *Dactylioceras* can be found in the *Treatise on Invertebrate Paleontology*, vol. L, p. 252. They are not discussed here,

for this description is concerned with only a single specimen of one of the earliest known species of *D. (Dactylioceras)*, and with abundant faunas of the subgenus *Orthodactylites*.

***Dactylioceras (Dactylioceras) pseudocommune* Fucini**

Pl. 1, fig. 1

- 1876 *Stephanoceras holandrei* (d'Orbigny) ; Tate & Blake : 172, 299-300.
 1935 *Dactylioceras pseudocommune* Fucini : 86, pl. 9, figs. 1-3.
 1935 *Dactylioceras pseudocrassulosum* Fucini : 87, pl. 9, figs. 6-8.
 1935 *Dactylioceras peloritenum* Fucini : 88, pl. 9, figs. 14, 15.
 1935 *Dactylioceras subholandrei* Fucini : 89, pl. 9, fig. 17.
 1935 *Dactylioceras inaequicostatum* Fucini : 89, pl. 9, fig. 16.
 ? 1966 *Dactylioceras mirabile* Fucini ; Fischer : 24, pl. 1, fig. 6 ; pl. 4, fig. 1.
 1966 *Dactylioceras pseudocommune* Fucini ; Fischer : 26, pl. 1, fig. 5 ; pl. 4, figs. 3, ? 6.
 1971 *Dactylioceras (Dactylioceras) pseudocommune* Fucini ; Pinna & Levi-Setti : 37, pl. 1, fig. 8.

MATERIAL. One specimen, Institute of Geological Sciences, London, GSM 22568, from the old ironstone mine at Hob Hill (NZ 653203), near Saltburn. Paltum Subzone, lower part. R. Tate collection.

DESCRIPTION. As discussed elsewhere (p. 246) this specimen almost certainly came from the Top Main Dogger and, from low in the Paltum Subzone only just above the base of the Upper Lias, is the oldest well-preserved *Dactylioceras* known in Britain.

It consists of one-third of a whorl of approximately 65 mm diameter ending in a broken aperture, and parts of the next two inner whorls are attached. The whorls are evolute, and the whorl section has flat sides and a broadly arched venter. Near the aperture the whorl height is 16.3 mm, and the whorl breadth is 14.5 mm. The ribs are high, sharp and straight ; most bifurcate at a small ventro-lateral tubercle, and the ribs then curve forwards and are continuous across the venter. Occasional ribs remain single : there are 14 bifurcating and 2 single ribs on the outer whorl of the fragment, giving a total of 30 secondary ribs on the venter. The umbilical seam just touches the ventro-lateral tubercles on the next inner whorl, and the secondaries are concealed. No traces of septae or suture-lines are to be seen on any of the whorls.

Reference is made to *Dactylioceras* s.s. because of the predominance of bifurcating ribs and ventro-lateral tubercles, and lack of the annular ribbing of *Orthodactylites*. The earliest group of species of *Dactylioceras* is best known from Taormina, Sicily, from the descriptions of Fucini (1935), and there is now good evidence from that area and other parts of Italy (see p. 271) that the group marks the base of the Tenuicostatum Zone. Specimens are common and it is probable that 2 species of *Dactylioceras* s.s. and 2 of *D. (Orthodactylites)* are present (Pinna & Levi-Setti 1971 : 90). The Hob Hill ammonite compares closely with the lectotype of *D. pseudocommune* Fucini (1935 : pl. 9, fig. 1). Nine other specimens figured by Fucini (see synonymy above) are considered to be conspecific, for all have low-density, straight ribs bifurcating at ventro-lateral tubercles. Other species from the same fauna are *D. (D.) simplex* Fucini (1935 : 86, pl. 9, figs. 4, 5) which has trifurcating ribs, and

therefore many more secondaries, and *D. (Orthodactylites) mirabile* and *polymorphum* Fucini, both with bifurcating and single ribs. *D. (D.) pseudocommune* also occurs in northern Italy (Pinna & Levi-Setti 1971 : 89, pl. 1, fig. 8), apparently low in the Tenuicostatum Zone, and the single figured specimen closely resembles the Hob Hill ammonite. Ammonites belonging to the same group of species occur at Kammerker, Austria, but in Fischer's (1966) description the Tenuicostatum Zone is dealt with as a single unit and the divisions into species are not based on stratigraphical associations. Some specimens (e.g. Fischer 1966 : pl. 4, figs. 1, 3, 6) do appear to be *D. (D.) pseudocommune*. Other possible occurrences in Algeria and Portugal are not supported by figured specimens. The group is mainly Mediterranean in distribution, and the Hob Hill specimen is the first record in north-west Europe. Its age in Yorkshire, at the base of the Paltum Subzone of the Tenuicostatum Zone, is good confirmation of the basal Tenuicostatum Zone age of this earliest group of species of *Dactylioceras* in Italy.

Dactylioceras sp. indet.

The existence of *Dactylioceras* in other parts of the Paltum Subzone is indicated by two specimens that are included here for record purposes.

1. A 36 mm diameter crushed *Dactylioceras* s.l. was found on the upper surface of bed 3 on the east side of Kettleness. Although poorly preserved, fairly widely spaced primary ribs and approximately twice as many secondary ribs can be seen, and it may belong to the earliest known group of species of *Dactylioceras* discussed above.

2. The impression of a venter of a *Dactylioceras* s.l. preserved solid, presumably in a nodule, was seen at about the middle of bed 6 in the bank of a stream at Hutton Lowcross (NZ 604134). The impression did not extend as far as the ventro-lateral angle.

Subgenus **ORTHODACTYLITES** Buckman, 1926

TYPE SPECIES : *O. directum* Buckman, 1926, by original designation.

SYNONYMS : *Kryptodactylites* Buckman, 1926 (type species : *Ammonites semicelatus* Simpson, 1843, by original designation); *Tenuidactylites* Buckman, 1926 (type species : *Ammonites tenuicostatus* Young & Bird, 1822, by original designation).

DIAGNOSIS. *Dactylioceras* with annular, rectiradiate or prorsiradiate ribs. Rib-density moderate to high, occasionally distantly ribbed on some whorls. Single ribs as well as bifurcating ribs occur commonly at some growth stage. Whorl shape varies from compressed to highly depressed. Ventro-lateral tubercles or spines may occur on forms with depressed whorls, and ribs may be looped to them in fibulate style.

DESCRIPTION. *Orthodactylites* is a subgeneric name for a group of species, occurring mainly in the Tenuicostatum Zone, that have annular ribs, some of which are single (i.e. not bifurcating) at least at some growth stage. Five species are found in British rocks. The type species *O. directum* Buckman (synonym : *O. mitis*

Buckman, 1927) occurs in the Transition Bed and the Marlstone Rock Bed from Lincolnshire to Gloucestershire, and is the only English species that does not occur in Yorkshire. The four Yorkshire species are *D. (O.) crosbeyi* (Simpson, 1843), *D. (O.) clevelandicum* sp. nov., *D. (O.) tenuicostatum* (Young & Bird, 1822) and *D. (O.) semicelatum* (Simpson, 1843). They are confined to the Tenuicostatum Zone and the type specimens of all four come from the Yorkshire Grey Shales. The last two species also occur in other parts of England, but the description below is concerned only with the Yorkshire occurrences. The earliest species of *Orthodactylites* are *D. (O.) mirabile* and *polymorphum* Fucini, originally described from Sicily (Fucini 1935), and also known from northern Italy, Austria and probably Algeria and Portugal (Pinna & Levi-Setti 1971: 37). In northern Italy and Austria their age is known to be Tenuicostatum Zone, but in Sicily their age is not accurately determinable and they may also occur in the top of the Spinatum Zone. The last species of *Orthodactylites* (as yet undescribed) occurs in the Exaratum Subzone in England.

***Dactylioceras (Orthodactylites) crosbeyi* (Simpson)**

Pl. 1, figs. 2-4; Pl. 2, figs. 1-4

1843 *Ammonites crosbeyi* Simpson: 22.

1855 *Ammonites crosbeyi* Simpson: 58.

1884 *Ammonites crosbeyi* Simpson: 90.

1912 *Coeloceras crosbeyi* (Simpson); Buckman: pl. 60.

? 1957 *Dactylioceras pseudosemicelatum* Maubeuge: 193, pl. 3, fig. 6.

? 1957 *Dactylioceras podagrosium* Maubeuge: 193, pl. 4, fig. 7.

TYPE. The holotype is Whitby Museum no. 134, and was figured by Buckman (1912: pl. 60). It comes from bed 18 of the Grey Shales, from a locality not known more accurately than "Whitby". Dimensions (in the order: whorl height, whorl breadth, umbilical width): at 74 mm diameter: 23.5 (0.32), —, 32.5 (0.44); at 48 mm diameter, whorl breadth is 24.7 mm (0.51); 69 ribs at 76 mm diameter.

DISTRIBUTION. Clevelandicum Subzone. Occurs only in Grey Shales bed 18, from which 69 specimens were collected (list on p. 241).

DIAGNOSIS. Whorls one-third to one-quarter involute, large whorl height, moderately wide umbilicus. Whorl section varies from sub-circular with approximately equal height and breadth, to highly depressed, where breadth/height ratio is up to 2.3 at diameters of 50 to 70 mm. Venter of depressed forms very wide and arched, and small ventro-lateral tubercles formed. Body chamber always becomes more compressed. Adult size 84 to 130 mm diameter, length of adult body chamber 15/16 to 17/16ths of a whorl. Ribs straight, slightly prorsiradiate, bifurcating or single, very variable in density.

DESCRIPTION. This species occurs only in bed 18, preserved in small calcareous nodules, or calcified masses of a few ammonites lying at all angles, at a single horizon at the middle of that bed. The preservation is only moderate, for in most cases the body chamber is preserved solid on one side and partly crushed on the other, while the inner whorls are crushed, distorted or missing. Only rarely are the inner

whorls preserved solid, and few specimens are sufficiently well preserved for measurements of whorl proportions and rib counts to be made.

D. (O.) crosbeyi is characterized by fairly high and thick whorls, about one-third to one-quarter involute (so that the umbilicus is moderately wide), and by fine to moderate rib-density. Some specimens, especially those with depressed whorls, have small ventro-lateral tubercles on all whorls except the final one, but others have no tubercles. Nine of the specimens collected have complete, adult body chambers, and the diameter at the final mouth border varies between 84 and 130 mm (average 101 mm). The length of the complete body chamber in six specimens varies between 15/16 and 17/16ths of a whorl. In all of them the final whorl has height and breadth about equal, or is slightly more compressed, and the ribs are moderate to dense (80–90 on the final whorl) with single and bifurcating ribs usually alternating, but more ribs become single near the end of the body chamber. Two examples with body chambers are figured in Pl. 1, fig. 2 and Pl. 2, fig. 2; some have inner whorls similarly compressed and fine-ribbed (e.g. Pl. 1, fig. 4), but others show great variation, and there is apparently complete gradation to highly depressed coronate inner whorls, in which the whorl breadth is probably greater than in any other Dactylioceratid ammonites. Three coronate inner whorls are figured in Pl. 2, figs. 1, 3 and 4; in the largest, at a diameter of about 70 mm, the whorl height is 18.5 mm, the breadth about 42 mm, giving a whorl breadth/height ratio of 2.3. The other two have ratios of 2.25 and 2.1 at smaller diameters. These inner whorls have small ventro-lateral tubercles or spines. The body chambers of such specimens become more compressed and the tubercles are lost (Pl. 1, fig. 3), and they are similar to the body chambers of specimens with compressed inner whorls. A collection with this large amount of variation is referred to only one species because they all come from a single horizon of nodules in a succession that is not condensed, there is complete gradation in variation between the markedly different end forms, and the adult body chambers are similar with a much smaller amount of variation.

D. (O.) crosbeyi has higher and thicker whorls and is more involute than *D. (O.) clevelandicum* or *tenuicostatum*. It has fewer ribs than the latter species, but is largely similar in rib-density to the former species. Differences from *D. (O.) semicelatum* are less marked, but the whorl height in *crosbeyi* is somewhat higher, overlapping only the upper half of the variation in *D. (O.) semicelatum*, and the holotype of *crosbeyi* has higher whorls than any *semicelatum*. Correspondingly the umbilical width is generally smaller in *crosbeyi* and the amount of involution more. The thick-whorled examples of *D. crosbeyi* are much thicker than any other species, and the holotype lies on the higher border of the range of variation in *clevelandicum* and *semicelatum* (see Text-fig. 5).

The only possible record of *D. (O.) crosbeyi* outside Yorkshire is the two specimens figured by Maubeuge (1957: 193, pl. 3, fig. 6; pl. 4, fig. 7) as the holotypes of *D. pseudosemicelatum* and *D. podagrosom* from eastern France. Without larger specimens from the same bed these two are difficult to determine, but they do appear to have thick whorls and non-tuberculate ribs like some specimens of *D. crosbeyi*, so it is possible that they are synonyms of that species.

Interpretation of *Ammonites annulatus* J. Sowerby, 1819

It has been stated previously by Sylvester-Bradley (1958: 67) and Howarth (1962: 410) that *D. crosbeyi* is a synonym of *Ammonites annulatus* J. Sowerby (1819: 41, pl. 222, fig. 5 only), when the latter species is restricted to its lectotype as selected by Oppel (1856: 255). This is not correct, for that lectotype is a fine specimen of *Nodicoeloceras crassoides* (Simpson, 1855) from bed 18/19, Falciferum Subzone, of the Ilminster-Barrington/Stocklinch succession. Its matrix agrees with that of other ammonites collected from that bed, and it is considerably different in matrix and morphology from specimens of *Dactylioceras* (*Orthodactylites*) that come from the thin representative (beds 1 and 2) of the Tenuicostatum Zone in that area. It is a large specimen with a complete adult body chamber $1\frac{1}{4}$ whorls long, on which the bifurcating ribs of earlier whorls give way to an alternation of bifurcating and single ribs. In this respect the last whorl resembles *Orthodactylites*, but it differs from *D. (O.) crosbeyi* in having thick inner whorls with a rounded cross-section and no tubercles. Sowerby's specific name *annulatus* cannot be used instead of *crassoides*, because it is a junior homonym of *Ammonites annulatus* Schlotheim, 1813.

***Dactylioceras (Orthodactylites) clevelandicum* sp. nov.**

Pl. 3, figs. 1-3; Pl. 4, figs. 1, 2; Pl. 5, fig. 3

TYPE. The holotype is C.77017 (Pl. 3, fig. 1) from bed 19b at Holmsgrove Sand. It is a complete specimen with 13/16ths of a whorl of body chamber ending in a contracted mouth border at 79 mm diameter, and has the following dimensions: at 77 mm diameter: 17.0 (0.22), 17.2 (0.22), 44.5 (0.58); 85 ribs at 78 mm diameter, 71 at 66 mm, 65 at 58 mm, 52 at 30 mm, 46 at 21 mm.

DISTRIBUTION. Clevelandicum Subzone. Grey Shales bed 19b, from which 199 specimens were collected.

DIAGNOSIS. Whorls evolute, small whorl height, wide umbilicus. Whorl section varies from rounded with equal height and breadth, to depressed with breadth/height ratio of up to 1.7 at 50 to 70 mm diameter. Ribs straight, recti-radiate, single and bifurcating, highly variable moderate to low rib-density. Ventrolateral tubercles or spines and fibulate ribbing occurs on some depressed whorls. Adult body chamber with many single ribs, no tubercles, more compressed than depressed inner whorls. Adult size 67 to 112 mm diameter, length of body chamber 13/16 to 16/16ths of a whorl.

DESCRIPTION. This species occurs in large numbers in calcified masses at the same horizon as the thin red-weathering nodules of bed 19b. All the exposures of that bed yielded some specimens, but particularly good localities from which large collections were made are the east side of Kettleness and Holmsgrove Sand. Several specimens are usually clustered together, all in different orientations, and calcification is confined to the immediate vicinity of the ammonites so that substantial nodules are not formed. Preservation is usually very good, with inner whorls and most of the body chamber solid and intact in many specimens. Such good material

has enabled whorl dimensions to be measured in 40 specimens and rib counts on 55 specimens.

D. (O.) clevelandicum is very evolute, with little overlap of the whorls, and so has a consistently small whorl height and wide umbilicus (Text-fig. 5). However, it shows a large amount of variation in whorl breadth and in rib-density (Text-fig. 6). The holotype has compressed whorls and a moderate to high rib-density. Other specimens, similarly compressed, have fewer ribs (Pl. 4, fig. 1), and there is then a complete series of gradations involving increasing whorl breadth and appearance of tubercles (Pl. 5, fig. 3; Pl. 3, fig. 3), ending with highly depressed tuberculate inner whorls (Pl. 3, fig. 2; Pl. 4, fig. 2). In the latter type the adult body chamber reverts to a non-tuberculate more compressed form, and the whorl thickness near the end of the body-chamber may be less than that of the previous whorl. In highly depressed specimens the ventro-lateral tubercles are spinose and fibulate. This large amount of variation in whorl thickness and rib-density is shown in Text-figs. 5 and 6; measurements from specimens are scattered evenly over the graphs from which these diagrams were drawn showing that the variation is continuous, though there are more moderate to finely ribbed specimens (like the holotype), than depressed, tuberculate specimens. The adult body chamber ends in a slightly contracted mouth border, and in 17 adults the diameter at the mouth border varies between 67 and 112 mm (average 85 mm). The length of these body chambers varies between 13/16 and 16/16ths of a whorl.

D. (O.) clevelandicum differs from *crossbeyi* and *semicelatum* in having slender more evolute whorls, and larger spinose tubercles on those with depressed inner whorls. It does not differ from either species in rib-density. *D. (O.) tenuicostatum* has slender evolute whorls, is always compressed and is more densely ribbed than *clevelandicum*; there is little overlap in the rib-density variation of the two species. *D. (O.) clevelandicum* is not known from outside Yorkshire.

***Dactylioceras (Orthodactylites) tenuicostatum* (Young & Bird)**

Pl. 5, figs. 1, 2; Pl. 6, figs. 2, 3

- 1819 *Ammonites annulatus* J. Sowerby : 41, pl. 222, fig. 1 only (*non* Schlotheim, 1813).
- 1822 *Ammonites tenuicostatus* Young & Bird : 247, pl. 12, fig. 8.
- 1828 *Ammonites annulatus* Sowerby ; Young & Bird : 253, pl. 12, fig. 11.
- 1884 *Stephanoceras annulatum* (J. Sowerby) ; Wright : 475, pl. 84, figs. 7, 8.
- 1920 *Dactylioceras tenuicostatum* (Young & Bird) Buckman : pl. 157.
- 1927 *Tenuidactylites tenuicostatus* (Young & Bird) Buckman : pl. 157A.
- 1933 *Dactylioceras tenuicostatum* (Young & Bird) ; Arkell : pl. 32, fig. 6.
- 1956 *Dactylioceras tenuicostatum* (Young & Bird) ; Arkell : pl. 33, fig. 6.
- 1957 *Dactylioceras tenuicostatum* (Young & Bird) ; Maubeuge : 208, figs. ? 41, 42, 43.
- 1961 *Dactylioceras tenuicostatum* (Young & Bird) ; Dean, Donovan & Howarth : pl. 72, fig. 1.

TYPE. The holotype is known to be lost (Howarth 1962a : 116). The neotype, here designated, is C.77182 (Pl. 5, fig. 1) from bed 22 exposed immediately east of Port Mulgrave harbour. It is a complete adult with a body chamber 14/16ths of a whorl long, ending in a contracted aperture at 89 mm diameter. Its dimensions

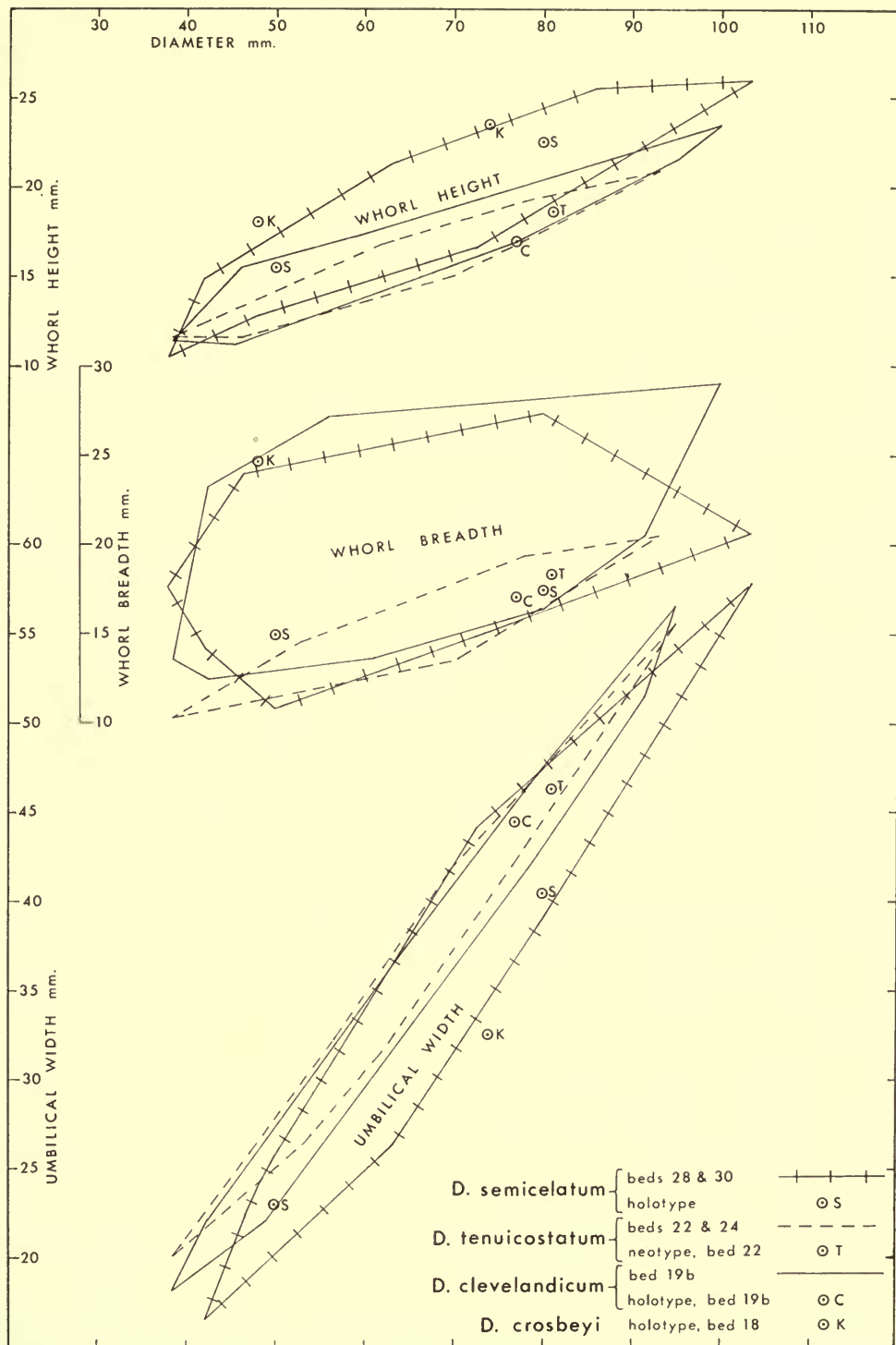


FIG. 5. Envelopes of scatter diagrams of whorl dimensions of Grey Shales species of *Dactylioceras* (*Orthodactylites*), plotted from measurements from 34 specimens of *D. (O.) semicelatum*, 31 of *D. (O.) tenuicostatum* and 41 of *D. (O.) clevelandicum*.

are : at 81 mm diameter : 18.7 (0.23), 18.4 (0.23), 46.4 (0.57) ; 123 ribs at 85 mm diameter, 108 at 75 mm, 100 at 65 mm, 81 at 48 mm, 64 at 30 mm.

DISTRIBUTION. *Tenuicostatum* Subzone. Grey Shales beds 20–26, from which 179 specimens were collected.

DIAGNOSIS. Whorls evolute, small whorl height, wide umbilicus, whorl breadth always slightly less than or equal to whorl height. No depressed forms. Ribs straight, fine, approximately rectiradiate, but prorsiradiate on inner whorls, single or bifurcating, high but variable rib-density. No tubercles. Adult size 72 to 105 mm diameter, length of body chamber 13/16 to 18/16ths of a whorl.

DESCRIPTION. The holotype was Whitby Museum no. 81, which is now lost, and there is no evidence for the existence of any other specimens in the type series. Identifications of this widely quoted species have been based on the well-preserved Whitby topotypes figured by Wright (1884 : pl. 84, figs. 7, 8), Buckman (1920 : pl. 157 ; 1927 : pl. 157A) and Dean, Donovan & Howarth (1961 : pl. 72, fig. 1). There is no doubt that these four topotypes came from beds 22 or 24 of the Yorkshire coast Grey Shales, and one of them, the specimen figured by Buckman (1920 : pl. 157), was said to be the neotype by Dean, Donovan & Howarth (1961 : 476). This neotype designation was defective in several ways : it did not fulfil the conditions of Art. 75 (c) (1), (5) and (6) of the Code of Zoological Nomenclature, because the characters differentiating the species were not given, the specimen was insufficiently documented, and it is now thought to be lost. The position can be retrieved by formally designating C.77182 as neotype, a specimen collected by myself just east of Port Mulgrave harbour. The exact horizon and locality of Young & Bird's holotype is not known, but it must have come from bed 22 or 24 of the Yorkshire coast Grey Shales, so C.77182 is a suitable specimen to be a neotype, especially as it is a well-preserved complete adult showing average characters for the species.

Almost all the small spherical nodules of beds 22 and 24 at all the localities contain a single specimen of *D. (O.) tenuicostatum* lying horizontally through the centre. Rarely nodules contain two or more smaller specimens. The nodule is generally larger than the ammonite it contains, and preservation is excellent, with all whorls up to the final mouth border intact. The inner whorls of some specimens are partly pyritized.

D. (O.) tenuicostatum has slender, evolute whorls with a small whorl height and a wide umbilicus. The whorl breadth is equal to or slightly less than the whorl height, and there are no examples with depressed whorls. In this respect it shows much less variation than any of the other species described here (Text-fig. 5), all of which have variants with depressed whorls. In rib-density, however, *tenuicostatum* has as much variation as the other species (Text-fig. 6). Sufficient measurements were made for the faunas from beds 22 and 24 to be plotted separately, and it can be seen from Text-fig. 6 that specimens in bed 24 have a slightly higher average rib-density than those in bed 22, although there is a very large percentage overlap between the two. The amount of variation in rib-density in *tenuicostatum* is just as large as in *clevelandicum*. There are no tubercles in *tenuicostatum*. The

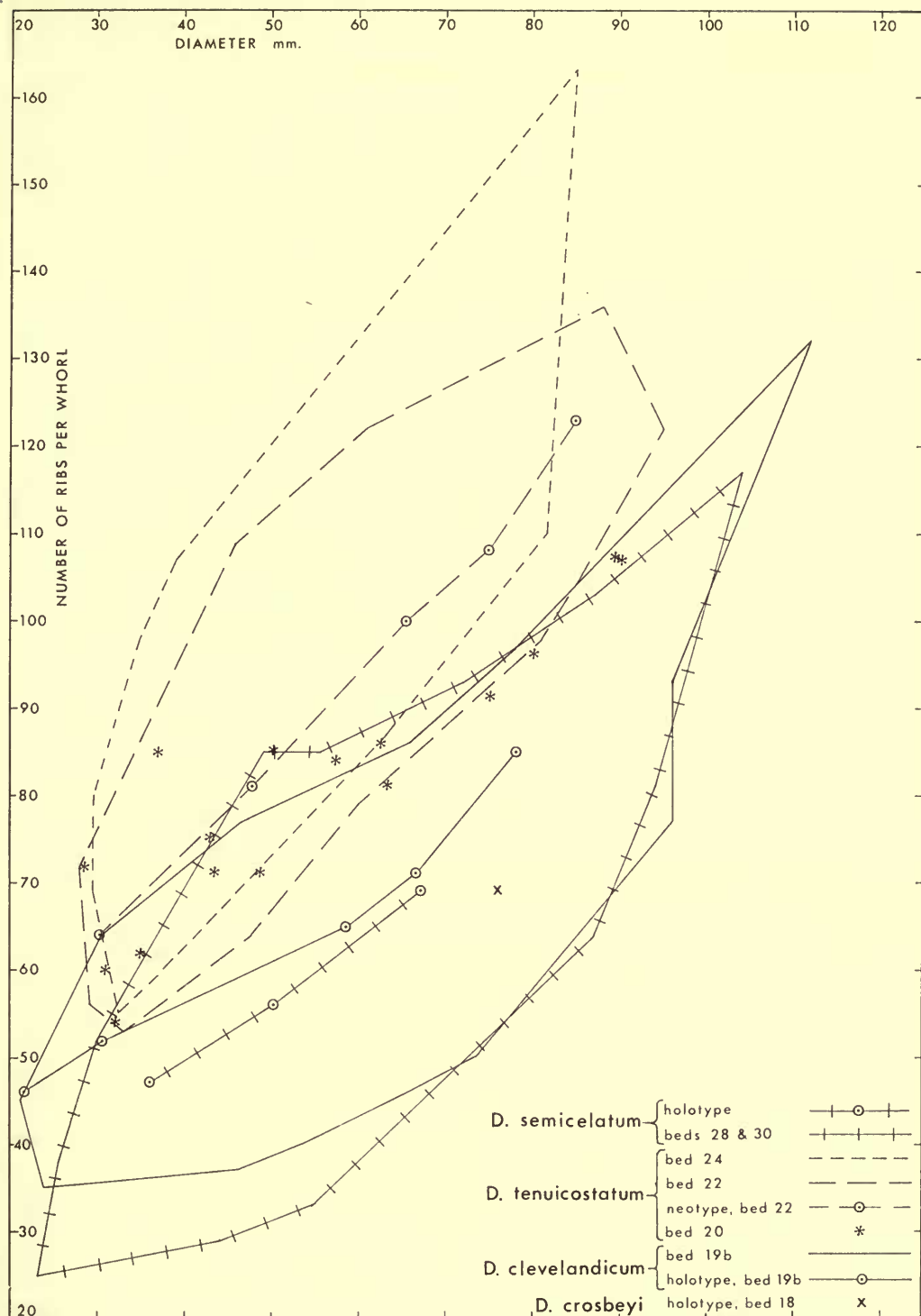


FIG. 6. Envelopes of scatter diagrams of number of ribs per whorl of Grey Shales species of *Dactylioceras* (*Orthodactylites*), plotted from 136 readings from 48 specimens of *D.* (O.) *semicelatum*, 104 readings from 45 *D.* (O.) *tenuicostatum* from bed 24, 89 readings from 37 from bed 22, 17 readings from 7 from bed 20, and 122 readings from 49 *D.* (O.) *clevelandicum* (total of 468 readings from 186 specimens).

average size of 18 complete adults from beds 22 and 24 is 88 mm diameter at the mouth border, the range being 72 to 105 mm, and there is no difference in the size range of specimens from the two beds. The length of the adult body chamber varies between 13/16 and 18/16ths of a whorl. The neotype (Pl. 5, fig. 1), from bed 22, is approximately average in adult size, length of body chamber and all whorl dimensions (Text-fig. 5); its rib-density is near to average for bed 22, and slightly less than average for bed 24, but well within the range of variation. One of the most densely ribbed specimens from bed 24 is figured in Pl. 6, fig. 2; it has 163 ribs on the whorl ending at 85 mm diameter, and a small portion of its final mouth border preserved at 90 mm diameter, the body chamber occupying 14/16ths of the final whorl. Another specimen from bed 24 is figured in Pl. 5, fig. 2, it being one of the least densely ribbed examples found at that horizon, and with an adult mouth border at 72 mm diameter, it is one of the smallest adults of the species.

In bed 20 specimens are less well preserved, and although 39 were collected, many are only fragments of whorls. None of them differ in whorl dimensions from *D. (O.) tenuicostatum* or from the more compressed part of the *clevelandicum* population. Their rib-densities are plotted as individual points on Text-fig. 6, and they can be seen to fall generally within or above the small range of overlap between those two species. A few are less densely ribbed than the bed 22 population, but some are considerably more densely ribbed than the bed 19b population, so, as there are no examples with depressed whorls, the bed 20 population is referred to *D. (O.) tenuicostatum*. The best specimen from bed 20 is figured in Pl. 6, fig. 3. The few specimens in bed 21 are typical fine-ribbed *D. (O.) tenuicostatum*, and the flat nodules of bed 26 contain a few moderately well-preserved, very fine-ribbed specimens similar to those of bed 24.

D. (O.) tenuicostatum is more densely ribbed than any of the other species described here, and has consistently slender and evolute whorls which are never depressed.

Dactylioceras (Orthodactylites) semicelatum (Simpson)

Pl. 6, fig. 1; Pl. 7, figs. 1, 2; Pl. 8, figs. 1-4; Pl. 9, figs. 1-3

- 1819 *Ammonites annulatus* J. Sowerby : 41, pl. 222, fig. 2 only (*non* Schlotheim, 1813).
- 1843 *Ammonites semicelatus* Simpson : 20.
- 1855 *Ammonites semicelatus* Simpson : 50.
- 1884 *Ammonites semicelatus* Simpson : 81.
- 1911 *Dactylioceras semicelatum* (Simpson) Buckman : pl. 31.
- 1927 *Kryptodactylites semicelatus* (Simpson) Buckman : pl. 31A.
- 1957 *Dactylioceras semicelatum* (Simpson) and spp. ; Maubeuge : figs. 1-3, ? 18-21, 41, 42, 44, ? 46, 47, 48, ? 49, ? 58, ? 59 (1), 59 (2).
- 1957 *Dactylioceras pseudocrassoides* Maubeuge : 201, pl. 13, fig. 28.
- 1957 *Dactylioceras densicostatum* Maubeuge : 202, pl. 13, fig. 29.
- 1968 *Dactylioceras (Orthodactylites) semicelatum* (Simpson) ; Hoffmann : 6, pl. 2, figs. 1, 2.
- 1968 *Dactylioceras (Orthodactylites) wunnenbergi* Hoffmann : 7, pl. 1, fig. 1.
- 1968 *Dactylioceras (Orthodactylites) eikenbergi* Hoffmann : 8, pl. 1, fig. 2.
- 1971 *Dactylioceras (Orthodactylites) anguinum* (Reinecke) ; Pinna & Levi-Setti : 90, pl. 2, figs. 1, 2, 5.
- 1971 *Dactylioceras (Orthodactylites) semicelatum* (Simpson) ; Pinna & Levi-Setti : 90, pl. 2, figs. 3, 4, 15.

TYPE. The holotype is Whitby Museum no. 116, and was figured by Buckman (1911 : pl. 31). It is from bed 28 or 30 of the Grey Shales, and its locality is not known more accurately than "Whitby". Dimensions : at 80 mm diameter : 22.5 (0.28), ca. 17.5 (0.22), 40.5 (0.51) ; 69 ribs at 67 mm diameter, 56 ribs at 50 mm, 47 ribs at 36 mm.

DISTRIBUTION. Semicelatum Subzone. Grey Shales beds 28 to 32, from which 102 specimens were collected.

DIAGNOSIS. Whorls about one-quarter involute, moderate whorl height, moderate to wide umbilicus, whorl section elliptical with narrow venter in compressed forms, where whorl breadth is less than height, but rounded in depressed whorls, where breadth/height ratio is up to 1.8 at 50 to 70 mm diameter. Ribs straight, rectiradiate or prorsiradiate, single or bifurcating, moderate to low variable rib-density. Small ventro-lateral tubercles on depressed whorls. Adult body chamber more compressed than earlier whorls, with more single ribs and no tubercles. Adult size 75 to 120 mm diameter, adult body chamber occupies 11/16 to 14/16ths of a whorl.

DESCRIPTION. A small proportion of the nodules in bed 28 contain single specimens of *D. (O.) semicelatum*. The preservation is only moderately good, and the nodules are extremely hard with much pyritization of and around the ammonites, so that specimens are difficult to extract. They are usually large and fully grown, but occasionally several small examples are found in one nodule. The nodules of bed 30 are even harder and there is more pyritization, but ammonites occur in more of the nodules and are better preserved. When the nodules have been subjected to foreshore weathering they will crack along the surface of the ammonites, and a larger collection was obtained from bed 30, including some very well-preserved complete adults. From about the middle of bed 31 up to 0.30 m below the top of bed 32, crushed specimens occur commonly, especially in patches in the shell beds at the base of bed 32. A small pyritic mass in bed 32 contained several small solid inner whorls and fragments.

D. (O.) semicelatum is about one-quarter involute and has relatively high whorls, with a characteristic elliptical whorl section in many specimens. This whorl shape occurs in the more compressed individuals where the whorl breadth is greatest near the umbilicus, and decreases towards a narrowly rounded venter. There is a large amount of variation in whorl breadth, especially on the inner whorls, for all gradations are found between slender compressed whorls, in which the breadth/height ratio is about 0.8 at 50 mm diameter, to greatly depressed coronate whorls in which the ratio is as high as 1.8 at a similar size. In adult whorls the variation is much less, because specimens with depressed inner whorls become less depressed on the final whorl, where whorl breadth and height are almost equal. Rib-density is generally moderate, but is highly variable on inner whorls depending on the whorl shape. Compressed inner whorls have moderately dense ribs, while depressed inner whorls have a much lower rib-density. The rib-density variation for 48 specimens from beds 28 and 30 is shown in Text-fig. 5. Points are evenly scattered over the area of variation in that diagram. On depressed inner whorls ventro-lateral tubercles are formed. No differences could be detected between the populations of

beds 28 and 30. Fourteen complete adults have mouth diameters varying between 77 and 117 mm (average 94 mm), and the length of the body chamber varies between 11/16 and 14/16ths of a whorl.

A large complete adult from bed 30 with compressed whorls throughout and average rib-density is figured in Pl. 7, fig. 1. Another complete adult from the same bed figured in Pl. 9, fig. 1 has depressed, sparsely ribbed inner whorls, changing to a more compressed, more densely ribbed outer whorl. The inner whorls of four specimens from bed 30 are shown in Pl. 8, figs. 1-3 and Pl. 9, fig. 2 to illustrate the amount of variation in whorl shape and rib-density. The two end members of the series are very different, yet all intermediates occur between them. Two examples from bed 28 are illustrated: one, Pl. 6, fig. 1, is a normal compressed type with moderately dense ribs, while the other, Pl. 7, fig. 2, has only slightly fewer ribs, but has a much greater whorl breadth.

The crushed specimens throughout much of the thickness of beds 31 and 32 show the characters of *D. (O.) semicelatum* fairly clearly. Whorl thicknesses cannot be observed, but some specimens, such as that figured in Pl. 8, fig. 4 from the middle of bed 31, show clearly inner whorls with few ribs, small ventro-lateral tubercles and an original depressed whorl shape that is now crushed, changing to a high more compressed outer whorl with many more ribs. A specimen with average rib-density and probably with originally compressed whorls from the shell bed at the base of bed 32 is figured in Pl. 9, fig. 3.

D. (O.) semicelatum is more involute and has higher whorls than either *tenuicostatum* or *clevelandicum*. Differences between *semicelatum* and *crossbeyi* are less and there is some overlap in the variation of the two. *D. (O.) crossbeyi* as a whole is more involute, has higher whorls and is not as compressed as *semicelatum*, and it does not have the characteristic elliptical whorl shape and narrow venter. The extremely depressed variants of *crossbeyi* have much broader whorls than *semicelatum*. The adult body chambers of *crossbeyi* are shorter than any in *semicelatum*; this is probably a reflection of the usually stouter whorls of the former.

The widespread distribution of *D. (O.) semicelatum* in eastern France, Luxembourg and north-west Germany is described in detail in the section on correlation (pp. 268-270). A typical densely ribbed specimen was figured as the new species *D. densicostatum* by Maubeuge (1957: fig. 29) and another specimen (fig. 28) with a large whorl breadth and distant ribs, almost exactly like the inner whorls of Pl. 9, fig. 1, was made the type of *D. pseudocrassoides*. Two specimens from north-west Germany with larger than average whorl breadth and ribs of fairly low density were made the types of *D. wunnenbergi* and *D. eikenbergi* by Hoffmann (1968); both can be matched with specimens from bed 30 of the Grey Shales, and they are synonyms of *D. semicelatum*.

Family HILDOCERATIDAE Hyatt, 1867

The two Hildoceratid ammonites found in the Grey Shales are *Protogrammoceras paltum* (Buckman) in bed 3 and *Tiltoniceras antiquum* (Wright) in bed 32, both belonging to the subfamily Harpoceratinae. These species will be described in

detail in another paper, so only a short account of their occurrence and identification is given here.

Protogrammoceras paltum (Buckman)

- 1922 *Paltarpites paltus* Buckman : pl. 362A.
 1923 *Paltarpites paltus* Buckman : pl. 362B.
 1964 *Paltarpites paltus* Buckman ; Maubeuge & Rioult : 107-113, 6 figs.
 1966 *Paltarpites paltus* Buckman ; Maubeuge & Rioult : 305-308, 3 figs.

DISTRIBUTION. *Paltum* Subzone. Grey Shales bed 3, from which four specimens were obtained and the impressions of two further large specimens were seen.

DESCRIPTION. Two of the specimens collected are large and well preserved, and consist of one whole whorl, half septate and half body chamber in each case, with all the smaller whorls missing, and the final part of the body chamber missing. C.47972 from Runswick Bay has a maximum size of 175 mm diameter ; C.72521 from Hawsker Bottoms is 140 mm diameter. The other two specimens are poorly preserved : C.77262 from Hawsker Bottoms is crushed and has about three whorls up to about 100 mm diameter ; C.77296 from east Kettleness is a fragment of a small section of a whorl at about 180 mm diameter. In addition two poorly preserved external moulds seen in bed 3 at east Kettleness and Holmsgrove Sand were both about 200 mm diameter. This is probably the approximate size of complete adult specimens, for both the well-preserved specimens would have been about that size when complete. These Grey Shales specimens agree exactly with the holotype of *P. paltus* (Buckman 1922 : pl. 362A) which comes from layer P of the Junction Bed at Thorncombe Beacon, Dorset. A paratype from the same bed and locality (Buckman 1923 : pl. 362B) shows somewhat coarser ribs on the inner whorls, while a specimen from the Marlstone Rock Bed at South Petherton, Somerset (Buckman 1923 : pl. 363) has finer ribbing throughout but is probably conspecific. The examples from Luxembourg described by Maubeuge & Rioult (1964 ; 1966) are also exactly like the Dorset and Yorkshire specimens, and attain a size of 150 mm diameter about half-way along the body chamber.

Comparison of the holotype of *Paltarpites paltus* with the lectotype of *Protogrammoceras bassanii* (Fucini 1901 : 46, pl. 10, figs. 6a-c), the type species of *Protogrammoceras*, shows that there are no differences worthy of generic distinction, and so *Paltarpites* is a synonym of *Protogrammoceras*.

Tiloniceras antiquum (Wright)

- 1875 *Ammonites acutus* Tate : 204 (non J. Sowerby, 1813).
 1882 *Harpoceras antiquum* Wright : pl. 57, figs. 1-4.
 1883 *Harpoceras antiquum* Wright : 431.
 1884 *Harpoceras acutum* (Tate) Wright : 469, pl. 82, figs. 7, 8.
 1887 *Ammonites acutus* Tate ; Denckmann : 59, pl. 10, figs. 1-3.
 1887 *Ammonites capillatus* Denckmann : 60, pl. 1, fig. 7 ; pl. 4, fig. 3.
 1893 *Harpoceras schroederi* Denckmann : 110.
 1913 *Tiloniceras costatum* Buckman : viii.
 1914 *Tiloniceras costatum* Buckman : pl. 97, figs. 1-4.

DISTRIBUTION. Upper part of the Semicelatum Subzone. Abundant in bed 32, especially in two shell beds at the base, and about 450 specimens were collected, mainly as crushed groups attached to slabs of shale.

DESCRIPTION. The majority of the specimens in the shell beds are between 20 and 30 mm diameter, some are up to 50 mm, but only a few are larger, and the largest found is 100 mm diameter. Most have at least part of their body chambers, so in view of the much larger sizes attained by isolated specimens, the shell beds probably consist of immature specimens of 20 to 50 mm diameter. There is no evidence that any of them are adult. Though crushed, a number can be seen to have smoothly rounded, not angled, umbilical edges, especially in one specimen where a small part is pyritized and uncrushed. Only two larger specimens are known in Yorkshire. The one figured by Wright (1882: pl. 57, figs. 1-4) as the holotype of *T. antiquum* is a magnificent specimen about 190 mm diameter at the final mouth border, in which the septate whorls are crushed flat, and the body chamber is preserved solid and shows the rounded umbilical edge well. It came from Hawsker Bottoms. The second large specimen (C.50353) was collected by myself about 0.45 m below the top of bed 32 at east Kettlewell, and consists of most of a well-preserved solid body chamber, 130 mm diameter, also showing a smoothly rounded umbilical edge. This is the only feature that distinguishes *Tiltoniceras* from *Eleganticeras*, its successor in the Exaratum Subzone, which always has an angled umbilical edge.

The population of *Tiltoniceras* in the Transition Bed of the Midlands is exactly the same in morphology, and also consists largely of small immature specimens, with only very rare large adults. The specific name *Ammonites acutus* Tate, 1875, applied to them is pre-occupied by *A. acutus* J. Sowerby, 1813, so *Tiltoniceras antiquum* is the first available name for the species. *T. costatum* Buckman (1913), given to an individual with stronger ribs, is a synonym, for the rib strength and density shows a moderate amount of variation.

The synonymy given above is not complete. Only the English and first-described north-west German occurrences are listed. More recent descriptions of the German fauna and occurrences in north-east Siberia are discussed below in the section on correlation.

IV. ZONAL SUBDIVISIONS

The history of the nomenclature and synonymy of the Tenuicostatum Zone was discussed by Dean, Donovan & Howarth (1961: 476). Briefly, the zone was introduced as the "Zone of *Ammonites annulatus*" by Tate & Blake (1876: 168), and altered to the Zone of *Dactylioceras tenuicostatum* by Buckman (1910a: 85) who realized that Tate & Blake had mis-identified the index species. That index species was the ammonite known to Tate & Blake to be very common at about the middle of the Grey Shales. So the Yorkshire coast and the Grey Shales are the type area and formation for the Tenuicostatum Zone. Ammonites of the sub-genus *Orthodactylites* are characteristic of the zone, particularly the index species and the closely related *O. semicelatum*, which is now known to occur at a higher horizon. In the Midland counties of England the Transition Bed overlies the

Marlstone Rock Bed, and contains two ammonites commonly, *Dactylioceras* (*Orthodactylites*) *directum* (Buckman) and *Tiltoniceras* (*T. acutum* (Tate) and *T. costatum* Buckman, both now held to be synonyms of *T. antiquum* (Wright)). These Transition Bed ammonites were the basis of the *acutum* hemera of Buckman (1898: 450, table 1), the *Acutum* Zone of Walford (1899: 33), and the *directus* and *Tiltoniceras* hemerae of Buckman (1930: 41). The Transition Bed immediately overlies the Marlstone Rock Bed, which is traditionally of *Spinatum* Zone age because of the occasional occurrence of *Pleuroceras*, so *Tiltoniceras* and *D. (O.) directum* were thought to be the earliest ammonites of the *Tenuicostatum* Zone by Dean, Donovan & Howarth (1961: 476), and indeed the zone had been divided into a lower *Tiltoniceras acutum* Subzone and an upper *Dactylioceras tenuicostatum* Subzone by Arkell (1933: 165; 1956: 35). A similar sequence has recently been used in France, where the *Tenuicostatum* Zone has been divided into a lower "Tiltoniceras" Subzone and an upper *Semicelatum* Subzone (Mouterde *et al.* 1971: 82). But *Tiltoniceras* is now known to occur in the top part of the Yorkshire Grey Shales at the same level as *D. semicelatum* and above *D. tenuicostatum*, so the Transition Bed of the English Midlands belongs to the highest part of the *Tenuicostatum* Zone. It is not proposed to perpetuate the use of a species of *Tiltoniceras* as a subzonal index, because the species *acutum*, always used before, is pre-occupied and has to be replaced by *antiquum*, and *Tiltoniceras* is probably less widespread than the accompanying *D. semicelatum*, which is likely to prove a more useful index species.

On the basis of the sequence of ammonites found in the Yorkshire Grey Shales, the following four subzones are proposed for the *Tenuicostatum* Zone:

- (Top) Subzone of *Dactylioceras* (*Orthodactylites*) *semicelatum*
- Subzone of *Dactylioceras* (*Orthodactylites*) *tenuicostatum*
- Subzone of *Dactylioceras* (*Orthodactylites*) *clevelandicum*
- (Bottom) Subzone of *Protogrammoceras paltum*

The top of the *Tenuicostatum* Zone is drawn (as explained above, p. 239) to coincide with the top of the Grey Shales in Yorkshire, that is between the highest *D. semicelatum* and *Tiltoniceras* 0.30 m below the top of bed 32, and the appearance of *Eleganticeras* in bed 33; in fact the boundary is placed at the base of bed 33. The bottom of the *Tenuicostatum* Zone poses more difficult problems in Yorkshire because there are very few ammonites low in the zone. It has to be above the highest *Pleuroceras*, which is characteristic of the *Spinatum* Zone, and in a previous paper it was placed at a convenient lithological boundary, the top of the Ironstone Series (top of Kettleness bed 28, Howarth 1955: 156). Later work by Hallam (1967: 403) and Chowns (1966; and personal communication), mainly on the lithology, has suggested that the base of Kettleness bed 26, the "Sulphur Band", is a better base for the zone. This is above the highest *Pleuroceras* in bed 25 and marks a persistent and distinctive lithological change. It is now known that the single specimen of *Dactylioceras* (*D.*) *pseudocommune* from north-west Cleveland probably came from the Top Main Dogger, the next bed above the "Sulphur Band" and the top bed of the Ironstone Series, being probably equivalent to Kettleness beds 27 and 28 on the coast. This species belongs to the earliest group

of *Dactylioceras* that mark the base of the Tenuicostatum Zone in Italy, and the base of the zone in Yorkshire is drawn, therefore, at the bottom of the "Sulphur Band" (Kettleness bed 26) between the highest *Pleuroceras* and the lowest *Dactylioceras*, at a distinctive lithological change which is also the horizon of a non-sequence in north-west Cleveland (Chowns 1966: fig. 1). It is of interest that this specimen of *Dactylioceras* occurs in a bed that is equivalent to a horizon (bed 27) only about 0.60 m above *Pleuroceras hawskerense* at Kettleness, so that the earliest group of *Dactylioceras* to which it belongs can be shown to follow closely above the last *Pleuroceras* in Yorkshire.

The Paltum Subzone is proposed for the lowest part of the Tenuicostatum Zone, which in Yorkshire and several areas of south-west England contains large specimens of *Protogrammoceras paltum*. *Dactylioceras* is very rare at this level in England, and in practice the base of the subzone (and the zone) has to be drawn above the highest *Pleuroceras* of the Spinatum Zone. *Dactylioceras* (*Orthodactylites*) appears in force in Yorkshire at the base of the Clevelandicum Subzone, first with *D. (O.) crosbeyi*, followed by *D. (O.) clevelandicum*. This subzone has not so far been identified outside Yorkshire. The Tenuicostatum Subzone is marked by the range of the index species, *D. (O.) tenuicostatum*, a highly distinctive ammonite of widespread occurrence in England and elsewhere. The Semicelatum Subzone is similarly drawn to coincide with the range of its index species *D. (O.) semicelatum*, also a distinctive ammonite of widespread occurrence. The other common British *Orthodactylites*, *D. (O.) directum*, occurs in both the Tenuicostatum and Semicelatum Subzones in the Midlands and south-west England. *Tiltoniceras* occurs in the upper part of the Semicelatum Subzone in Yorkshire, but its distribution within the subzone is not known in other areas.

V. CORRELATION WITH OTHER AREAS

ENGLAND. The occurrence and subdivision of the Tenuicostatum Zone in other parts of England will be described in another paper. Comment here is confined to the observation that the Transition Bed of the Midlands belongs to the Semicelatum Subzone, and that the top part (? up to 1 m) of the Marlstone Rock Bed belongs to the Tenuicostatum Subzone.

NORTH-WEST GERMANY. The subdivisions proposed by Denckmann (1893) and other workers were summarized by Dean, Donovan & Howarth (1961: 477, 479). Later work by Hoffman & Martin (1960), Hoffmann (1960: 75, 76; 1968) and Lehmann (1968), including data from boreholes, has established that the zone is up to 7.5 m thick. Two rows of nodules occur, the Capillatum Nodules (after *Tiltoniceras capillatum* (Denckmann)) at the top, and the Siemensi Nodules (after *Lytoceras siemensi* (Denckmann)) 0.5–1.0 m below. From these Hoffmann (1968: 21) derived two divisions of the Tenuicostatum Zone, the Capillatum Subzone above and the Siemensi Subzone below. Lehmann (1968: 63) pointed out that *L. siemensi* also occurs in the Exaratum Subzone and is therefore unsuitable as an index species, and he combined the two into the Siemensi-Capillatum (= "Acutum") Subzone.

The following ammonites from the two rows of nodules have been figured, mainly under different specific names, all of which are considered to be synonyms of the species indicated below :

Capillatum Nodules :

Tiltoniceras antiquum—Hoffmann 1968 : pl. 4, fig. 3 ; pl. 5, figs. 2, 3.

Dactylioceras (Orthodactylites) semicelatum—Hoffmann 1968 : pl. 2, fig. 2.

D. (O.) directum—Hoffman 1968 : pl. 2, figs. 3, 4 ; pl. 3, fig. 1 (refigd. Lehmann 1968 : 46, pl. 17, fig. 6).

Siemensi Nodules :

Tiltoniceras antiquum—Hoffmann 1968 : pl. 3, fig. 4 ; pl. 4, figs. 1, 2 ; pl. 5, figs. 1, 4.

Dactylioceras (Orthodactylites) semicelatum—Hoffmann 1968 : pl. 1, figs. 1, 2 (examples with thick whorls) ; pl. 2, fig. 1.

D. (O.) directum—Hoffmann & Martin 1960 : pl. 9, fig. 5 ; pl. 10, figs. 2a, 2b.

Lytoceras siemensii—Hoffmann & Martin 1960 : pl. 10, fig. 1.

Tiltoniceras antiquum, *D. (O.) semicelatum* and *D. (O.) directum* occur in both rows of nodules, so they both belong to the Semicelatum Subzone, when compared with the succession now known from Yorkshire and with the ammonites in the Midlands Transition Bed. No definite specimens of *D. (O.) tenuicostatum* are known from the shales below the nodules. Some of the ammonites from the top 1.5 m of the 6.4 m of shales belonging to the Tenuicostatum Zone in the borehole were figured by Hoffmann & Martin (1960 : pl. 8, figs. 1–3 ; pl. 9, figs. 1–4) as *D. (O.) tenuicostatum*. They are all crushed and difficult to determine, but some appear to have the high whorls of *D. (O.) semicelatum*. Thus, all the Tenuicostatum Zone ammonites known so far in north-west Germany belong to the highest subdivision, the Semicelatum Subzone.

EASTERN FRANCE AND LUXEMBOURG. The development of the Tenuicostatum Zone has been described by Maubeuge (1948 ; 1952). The zone consists of shales and marls, with some limestone, and is thin (up to 1 m) in most places, but at Bettembourg, Luxembourg, a good section is exposed in two quarries and the zone is 4.9 m thick. The Dactylioceratidae were described in another paper by Maubeuge (1957), and in the following section of the beds at Bettembourg, the ammonites are my determinations of Maubeuge's figures :

(Shales, bituminous ; impressions of "*Dactylioceras cf. semicelatum*" at the base).

3 Shale, marly, closely laminated, 2.60 m.

Dactylioceras semicelatum (figs. 16, ? 18–21, 29, ? 58, ? 59 (1)).

D. directum (figs. 9 (2–5), 14, 24, 25, 27, 38, 52–56).

Dactylioceras sp. indet. (figs. 9 (1), 17, 22, 23, 26, 36, 37, 39, 45, 57, 62, 63).

2 Limestone, 0.50 m.

Dactylioceras directum (fig. 15).

D. semicelatum (fig. 41).

1 Shale, marly, 1.80 m.

Protogrammoceras paltum (Maubeuge & Rioult 1964 ; 1966).

Bed 3 belongs to the Semicelatum Subzone and contains several typical examples of the index species and of *D. directum*—the holotype of *D. densicostatum* Maubeuge (1957, fig. 29) is a typical *D. semicelatum*, the holotypes of *D. semicelatoides* (fig. 27) and *D. microdactyliiformis* (fig. 38) belong to *D. directum*, while the holotypes of *D. obliquecostatum* (fig. 36) and *D. mastodontoides* (fig. 57) are not specifically determinable. The limestone of bed 2 also appears to belong to the Semicelatum Subzone because of a *D. directum* (fig. 15) and a *D. semicelatum* (fig. 41—the whorl height is much too large for *D. tenuicostatum*) which it contains. *Protogrammoceras paltum* occurs at the base of bed 1 (Maubeuge & Rioult 1964: 112, footnote), and the three crushed specimens and the fragment of a large well-preserved body chamber that were figured by Maubeuge & Rioult (1964; 1966) agree exactly with those found in bed 3 of the Yorkshire Grey Shales. The base of bed 1 at Bettembourg can be referred to the Paltum Subzone. Ammonites of the Clevelandicum and Tenuicostatum Subzones have not been found.

The following ammonites from other areas were also figured by Maubeuge (1957): *Dactylioceras semicelatum*—figs. 1-3, 8, 28, 42, 44, ? 46, 47, 48, ? 49, 59 (2).

D. directum—fig. ? 43.

D. ? crosbeyi—figs. ? 6, ? 7.

Dactylioceras sp. indet.—figs. 4, 5, 10-13, 30-35, 40, 50, 51, 60, 61.

These include the holotype of *D. pseudocrassoides* (fig. 28) from Bourmont (Haute Marne), which agrees closely with the broad, distantly ribbed inner whorls of some specimens of *D. semicelatum* such as that figured in Pl. 9, fig. 1 from bed 30 of the Yorkshire Grey Shales. Two other specimens of *D. semicelatum* from Bourmont were also figured (figs. 8, 59 (2)). The type specimens of the two new species *D. novimagense* (fig. 35) and *D. lamellosum* (figs. 50, 51) are specifically indeterminate.

Finally two further new specific names are difficult to place: the holotypes of *D. pseudosemicelatum* (fig. 6) and *D. podagrosum* (fig. 7) are both from Audeloncourt (Haute Marne) and appear to be conspecific. All the other figured ammonites from Audeloncourt (figs. 4, 5, 60) are indeterminate, and give no indication of age. These two holotypes have broad whorls but no ventro-lateral tubercles; they might be examples of *D. crosbeyi*, and if this determination could be confirmed by better and larger specimens, it would be the only record of that species and of the Clevelandicum Subzone outside Yorkshire.

The records summarized above show that in eastern France and Luxembourg there is good evidence of the Semicelatum Subzone at many localities, the Paltum Subzone occurs at Bettembourg, the Clevelandicum Subzone may occur at one locality, but no evidence of the Tenuicostatum Subzone has yet been found.

AUSTRIA AND ITALY. The earliest known *Dactylioceras* are the four species *D. (D.) pseudocommune* and *simplex*, and *D. (Orthodactylites) mirabile* and *polymorphum*, all of Fucini (1935), first described from Taormina, Sicily, and assigned by him to the Domerian (Upper Pliensbachian). Their nomenclature was revised by Pinna & Levi-Setti (1971: 89-91), who also described examples from northern Italy, but without adding any stratigraphical data. More specimens from central and northern Italy were described by Cantaluppi & Savi (1968: 231) who claimed to have determined their age as Upper Domerian, and by Ferretti (1967; 1970)

who found them in a stratigraphical sequence marking the base of the Toarcian. Ferretti's evidence was that in two different areas the *Dactylioceras* fauna occurred only above faunas of *Emaciaticerases* and *Canavaria* which were typical of the top part of the Domerian, and the Domerian-Toarcian boundary could be accurately drawn between them. Specimens of *Protogrammoceras* (determined as "*Mercaticeras*" by Ferretti) accompanied the *Dactylioceras* and it was similar specimens that had led Cantaluppi & Savi (1968) to date their fauna as Domerian, but it is well known that *Protogrammoceras* ranges up as far as the top of the Tenuicostatum Zone. The sequence of ammonite faunas in the top half of the Domerian in the Mediterranean area that was used by Ferretti is best shown in Portugal (Mouterde 1967: 216-217) and Morocco (Dubar 1954: 24), where the following succession has been established:

- 4 *Dactylioceras* and *Protogrammoceras*. Base of Toarcian, Tenuicostatum Zone.
 - 3 Horizon with *Canavaria* (including "*Tauromeniceras*"), *Protogrammoceras* and *Pleuroceras spinatum*.
 - 2 Horizon with *Emaciaticerases*, *Canavaria* and *Protogrammoceras*.
 - 1 Horizon with *Lioceratoides*, *Protogrammoceras*, *Pleuroceras solare* and *P. spinatum*.
- Horizons 1-3 represent the Spinatum Zone of the north-west European Province because *Pleuroceras* occurs at most levels in Portugal, and they do not represent ammonite faunas that occur between the typical north-west European *Pleuroceras* and *Dactylioceras* faunas, as claimed by Ferretti (1970: 456).

The ammonites from Taormina, Sicily, that were described by Fucini, were existing museum specimens obtained mainly from screes without knowledge of their stratigraphical relationships. Fucini referred them all to the Domerian substage, an age assessment that was questioned by Arkell (1956: 210) who thought that the *Dactylioceratidae* were probably Toarcian. The most readily obtainable Taormina ammonites do come from screes, but some forms can be collected *in situ*, as was found when the author collected there in 1957. In fact three faunas were collected from single beds:

- 1 From a limestone 0.20 m thick in a quarry east of the Fontanelle ravine—*Arieticerases naxense* (Gemmellaro), *Emaciaticerases lottii* (Gemm.), *E. timaei* (Gemm.), *Fontanelliceras fontanellense* (Gemm.), *F. juliae* (Bonarelli), *Canavaria haugi* (Gemm.), *C. canavarii* (Gemm.) and *Protogrammoceras hoffmanni* (Gemm.). This is a rich mixed fauna of *Hildoceratidae* from horizon 2, the *Emaciaticerases* horizon.
- 2 From a marly limestone 0.30 m thick in the Fontanelle ravine—*Pleuroceras solare* (Phillips) (abundant), *P. spinatum* (Bruguière) and *Lioceratoides aradasi* Fucini. This association can be dated as horizon 1 from the presence of *Lioceratoides*, and the many specimens of *Pleuroceras solare* show that horizon 1 is equivalent to the Apyrenum Subzone of the Spinatum Zone of north-west Europe. This is probably the bed from which some of Fucini's (1924: pl. 1, figs. 5, 6, ? 3) specimens of *Pleuroceras* were obtained. Thus it can be shown again that the *Lioceratoides* horizon is not younger than the *Pleuroceras* faunas of north-west Europe.

- 3 From a marly limestone 0.15 m thick at Tirone Cliff, stratigraphically high in the succession—*Dactylioceras* (*D.*) *pseudocommune* Fucini and *D. (Orthodactylites) polymorphum* Fucini. It is significant that there were no accompanying ammonites with this, the only collection of *Dactylioceras* found *in situ*, and it can be concluded that, as in central and northern Italy, the earliest fauna of *Dactylioceras* occurs at a higher level than the typical Domerian Hildoceratidae, and that it marks the base of the Tenuicostatum Zone at the bottom of the Toarcian.

A similar fauna occurs at Kammerker, Austria, and has been described by Fischer (1966), who proposed the new specific name *D. triangulum* for specimens that are a close match for *D. pseudocommune*. *D. semicelatum* probably occurs higher in the Tenuicostatum Zone in Italy, for six specimens figured by Pinna & Levi-Setti (1971: 90, pl. 2, figs. 1–5, 15) seem to belong to that species, but the Kammerker specimen figured as *D. semicelatum* by Fischer (1966: 21, pl. 3, fig. 4) is a small indeterminate fragment.

PORTUGAL, SPAIN AND NORTH AFRICA. The Tenuicostatum Zone is probably well represented in Portugal and might attain a thickness of as much as 30 m. The occurrences are summarized by Mousterde (1967: 218) and several species of *Dactylioceras*, including *D. semicelatum*, are recorded. None are figured, nor are the accompanying Hildoceratidae determined as *Ovaticeras* cf. *ovatum*, *Eleganticeras* “*elegans*” (Y. & B.) and *Harpoceras capellinum*, all of which are post-Tenuicostatum Zone forms. Until the whole of this ammonite fauna is figured accurate assessment of the age is not possible. The zone is probably present in Spain, and descriptions that include records that might be Tenuicostatum Zone *Dactylioceratidae* were given by Behmel & Geyer (1966), Dubar, Elmi & Mousterde (1970) and Mousterde (1970). An occurrence of the Tenuicostatum Zone in Morocco with *Dactylioceras* has been recorded by Dubar (1954: 23).

The ammonite *Bouleiceras* occurs rarely in the Tenuicostatum Zone of Portugal and Spain, and also in Morocco. These are occurrences outside the main area for the *Bouleiceras* assemblage in West Pakistan, Arabia and east Africa, where species of *Protogrammoceras*, especially *P. madagascariense* (Thevenin), are the usual accompanying ammonites. The distribution of this assemblage is described in another paper (Howarth 1973). No *Dactylioceratidae* are known from the assemblage, and the age assessment is based on the presence of *Bouleiceras* in Portugal, and the presence of *Protogrammoceras*, which is known in the Tenuicostatum Zone, but not higher, in several areas of Europe.

EASTERN EUROPE. The occurrence of the Tenuicostatum Zone in Bulgaria has been summarized by Sapunov (1968: 140), and ammonites identified as *D. tenuicostatum*, *D. semicelatum* and *D. acanthus* were figured in an earlier paper (Sapunov 1963: 116–118, pl. 1, figs. 1–4). These come from a locality where the Tenuicostatum, Falciferum and Bifrons Zones occur in a condensed bed only 0.42 m thick. Although one of the figured specimens (Sapunov 1963: pl. 1, fig. 3) does appear to be a *D. semicelatum*, identification of *Dactylioceratidae* from condensed deposits is extremely difficult and uncertain. Records of species of *Tiltoniceras* from the

same condensed beds are not supported by figured specimens, but if correct they would prove to be an interesting easterly extension of the range of the genus, at present known only from England and north-west Germany in Europe.

No *Tenuicostatum* Zone ammonites have been found in Hungary. The presence of the *Tenuicostatum* Zone in Romania is shown by seven ammonites from the Brasov area figured by Popa (1970 : 90, figs. 1-7). The preservation is only moderate, and all could be examples of *D. semicelatum*, indicating the highest part of the zone, but one (Popa 1970 : fig. 1) might be a *D. tenuicostatum*, showing that a lower horizon may be present as well.

NORTH-EAST SIBERIA. The Upper Lias is well developed and rich in ammonites in the basin of the Omolon River (lat. 65° N, long. 161° E) especially in the area of its tributary, the River Kedon. Beds belonging to the *Tenuicostatum* Zone are shales with nodules up to 15-18 m thick; they overlie beds with late species of *Amaltheus*, probably of the *Spinatum* Zone, and are overlain by beds that contain good specimens of *Harpoceras exaratum* (Polubotko & Repin 1966 : pl. 1, fig. 7; Repin 1968 : pl. 45, figs. 2-4, pl. 47, fig. 1) indicating the Exaratum Subzone. The stratigraphy was first described by Dagis & Dagis (1965 : 15) who recorded *Ovaticeras propinquum* (Whiteaves), *Catacoeloceras* spp. and ? *Mercaticeras* from several levels within the 15 m of beds for which the term "Zone of *Ovaticeras propinquum*" was proposed. More localities were described the following year by Polubotko & Repin (1966 : 30), and examples of the "*Ovaticeras*" described and figured as a new species, *O. facetum* Polubotko & Repin (1966 : 45, pl. 1, figs. 4, 5, 8), came from the upper one-third of the zone. The zonal term was replaced by the "Zone of *Ovaticeras facetum*". More specimens of *O. propinquum* and *O. facetum* from the Omolon area were figured later by Repin (1968 : 115, 116, pl. 44, fig. 1; pl. 45, fig. 1, pl. 46, figs. 1, 2), together with two specimens identified as *Tiltoniceras* sp. (Repin 1968 : 116, pl. 44, figs. 2, 3). These two species of "*Ovaticeras*" contain some very well-preserved specimens up to 90 mm diameter, and the figured ones are all undoubted examples of *Tiltoniceras* that do not seem to differ from the English species *T. antiquum*. In fact precise matches for them can be found amongst the fauna of *T. antiquum* in the Transition Bed at Tilton, Leicestershire. ["*Ovaticeras propinquum* (Whiteaves) is a *Harpoceras* from the Lower Toarcian (? *Falci-ferum* Zone) of British Columbia."] The specimens figured by Repin as *Tiltoniceras* sp. are more heavily ribbed, and do not appear to differ from the typical *Harpoceras exaratum* microconchs figured by Repin (1968 : 117, pl. 45, figs. 2, 3) from the Exaratum Subzone.

A highly depressed Hildoceratid ammonite, that was probably the form recorded as ? *Mercaticeras* by Dagis & Dagis (1965), was described as the new genus *Arctomercaticeras* by Repin (1968a), which is here considered to be one of the last genera of the subfamily Arieticeratinae. The Dactylioceratidae from the *Tenuicostatum* Zone of the Omolon Basin were described by Dagis (1968 : 56-62, pl. 11, figs. 1-7) as two species of his new genus *Kedonoceras*. They came from near the base of the zone, well below the main occurrence of *Tiltoniceras*, and the genus was proposed for the depressed whorl shape, the presence of ventro-lateral tubercles, and the form of the suture-lines that largely reflect the cadicone shape of the shell. These

depressed forms are exactly like those found in all the Yorkshire Grey Shales species except *D. tenuicostatum*. Depressed specimens of *D. crosbeyi* from bed 18 such as those in Pl. 2, figs. 1, 3 compare very closely with *Kedonoceras comptum* Dagis (1968a: pl. 11, figs. 1, 2), and the generic name *Kedonoceras* could equally well be applied to the Yorkshire forms. For reasons given earlier the Yorkshire depressed forms are thought to be part of the variation within species of *Dactylioceras* (*Orthodactylites*), and it seems that *Kedonoceras* might well be placed in synonymy, even if the Siberian forms are specifically different, because some considerably less depressed forms occur as well (e.g. Dagis 1968: pl. 11, fig. 4).

The dating of *Tiltoniceras* as late Tenuicostatum Zone is confirmed, therefore, in north-east Siberia, where the Tenuicostatum Zone up to 18 m thick contains *Tiltoniceras* in the top one-third, indicating the Semicelatum Subzone, and depressed forms of *Dactylioceras* (*Orthodactylites*) near the base that closely resemble those occurring in the Clevelandicum Subzone.

WESTERN NORTH AMERICA. Small ammonites from the South Barrow borehole in north Alaska were figured as *Dactylioceras* cf. *semicelatum* and *D.* cf. *kanense* McLearn by Imlay (1955: 87, 88, pl. 10, figs. 6, 13, 14). They could well be Tenuicostatum Zone forms, but are somewhat small for definite identification. The Maude Formation of Skidegate Inlet, Queen Charlotte Islands, British Columbia, contains *Dactylioceras kanense* McLearn (1932: 59, pl. 4, figs. 1-7; pl. 5, figs. 6-9), which probably occurs at the same horizon as *Harpoceras propinquum* (Whiteaves) and *H. allifordense* McLearn. It is not possible to date this fauna in terms of European zones, although the two species of *Harpoceras* probably indicate the Falciferum Zone rather than the Tenuicostatum Zone. *D. kanense* is probably an *Orthodactylites*, judging from the rib pattern of the holotype (refigured Frebold 1964: pl. 7, fig. 4; Imlay 1968: pl. 3, fig. 12) and could be of Tenuicostatum Zone or Exaratum Subzone age. Age determinations are even more difficult for a series of *Dactylioceratidae* from Eastern Oregon and California figured mainly as various species of *Orthodactylites* by Imlay (1968: 30-32, pl. 3, figs. 1-16). Some of them (figs. 13-16) appear to have the tuberculation pattern of *Prodactylioceras*, but others (figs. 1, 2, 8, 11) have all the characters of *Orthodactylites*. The ammonite *Fanninoceras* occurs in the Nicely Shale Formation at or above the horizon of some of these *Dactylioceras*, and in view of the fact that *Fanninoceras* is now interpreted as a Lower Pliensbachian Oxynoticeratid, it seems that a re-assessment of the occurrence and age of all the ammonites in this formation is required. In particular, a ? *Dactylioceras* with widely spaced ribs (Imlay 1968: pl. 3, figs. 3-6) and *Fanninoceras* (pl. 8, fig. 21) come from the same locality, though their relative stratigraphical positions are not recorded. The genus *Arietoceras*, a typical Margaritatus and Spinatum Zone form, accompanies many of these ? *Orthodactylites* and ranges almost to the top of the Nicely Shale. If the association of genuine *Arietoceras* and *Orthodactylites* could be confirmed, and dated as Spinatum Zone, it would be the first definitely known occurrence of *Orthodactylites* below the Tenuicostatum Zone. Unfortunately Amaltheid ammonites, that would settle the date without question, are absent.

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PLATES

The photographs were taken by the author, and all specimens were given a thin coating of ammonium chloride.

All the figures are natural size.

PLATE 1

Dactylioceras (Dactylioceras) pseudocommune Fucini

FIG. 1. [Top Main Dogger, lower part of Paltum Subzone], old ironstone mine, Hob Hill, near Saltburn. R. Tate collection. Institute of Geological Sciences, London, GSM 22568.

Dactylioceras (Orthodactylites) crosbeyi (Simpson)

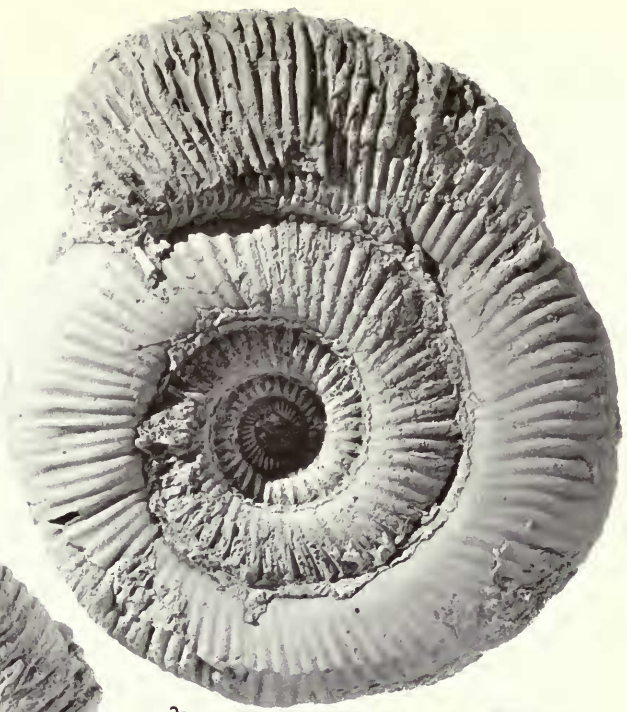
FIGS. 2-4. Grey Shales bed 18, Clevelandicum Subzone. Fig. 2, west of Port Mulgrave, C.47950 ; Fig. 3, Holmsgrove Sand, C.76908 ; Fig. 4, Runswick Bay, C.47913.



1a



1b



2a



3a



4a



4b



3b



2b

PLATE 2

Dactylioceras (Orthodactylites) crosbeyi (Simpson)
Grey Shales bed 18, Clevelandicum Subzone.

FIGS. 1, 2. East Kettleness, C.76890 and C.76886.

FIGS. 3, 4. Holmsgrove Sand, C. 76893 and C.76892.



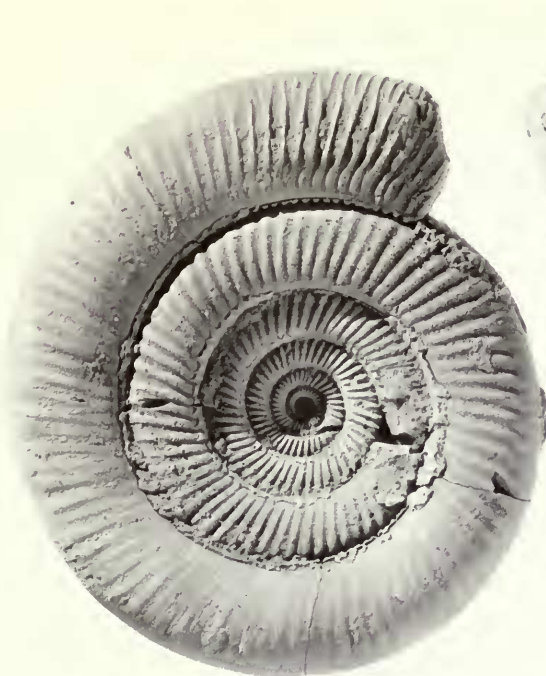
PLATE 3

Dactylioceras (Orthodactylites) clevelandicum sp. nov.

Grey Shales bed 19b, Clevelandicum Subzone.

FIGS. 1, 2. Holmsgrove Sand; Fig. 1. Holotype, C.77017; Fig. 2. C.76990.

FIG. 3. West of Port Mulgrave, C.76989.



1a



2a



1b



3a



3b



2b

PLATE 4

Dactylioceras (Orthodactylites) clevelandicum sp. nov.

Grey Shales bed 19*b*, Clevelandicum Subzone.

FIGS. 1, 2. Holmsgrove Sand, C.76997 and C.50419.

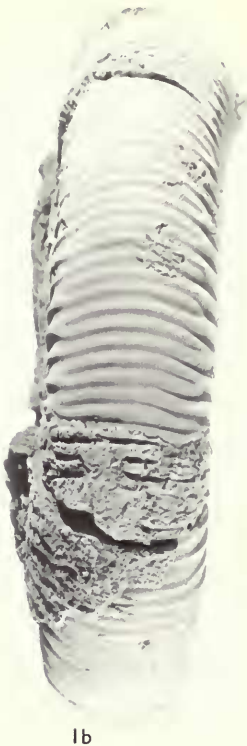


PLATE 5

Dactylioceras (Orthodactylites) tenuicostatum (Young & Bird)

FIG. 1. Neotype, Grey Shales bed 22, Tenuicostatum Subzone, west of Port Mulgrave, C.77182.

FIG. 2. Grey Shales bed 24, Tenuicostatum Subzone, east Kettleness, C.47927.

Dactylioceras (Orthodactylites) clevelandicum sp. nov.

FIG. 3. Grey Shales bed 19b, Clevelandicum Subzone, east Kettleness, C.76986.

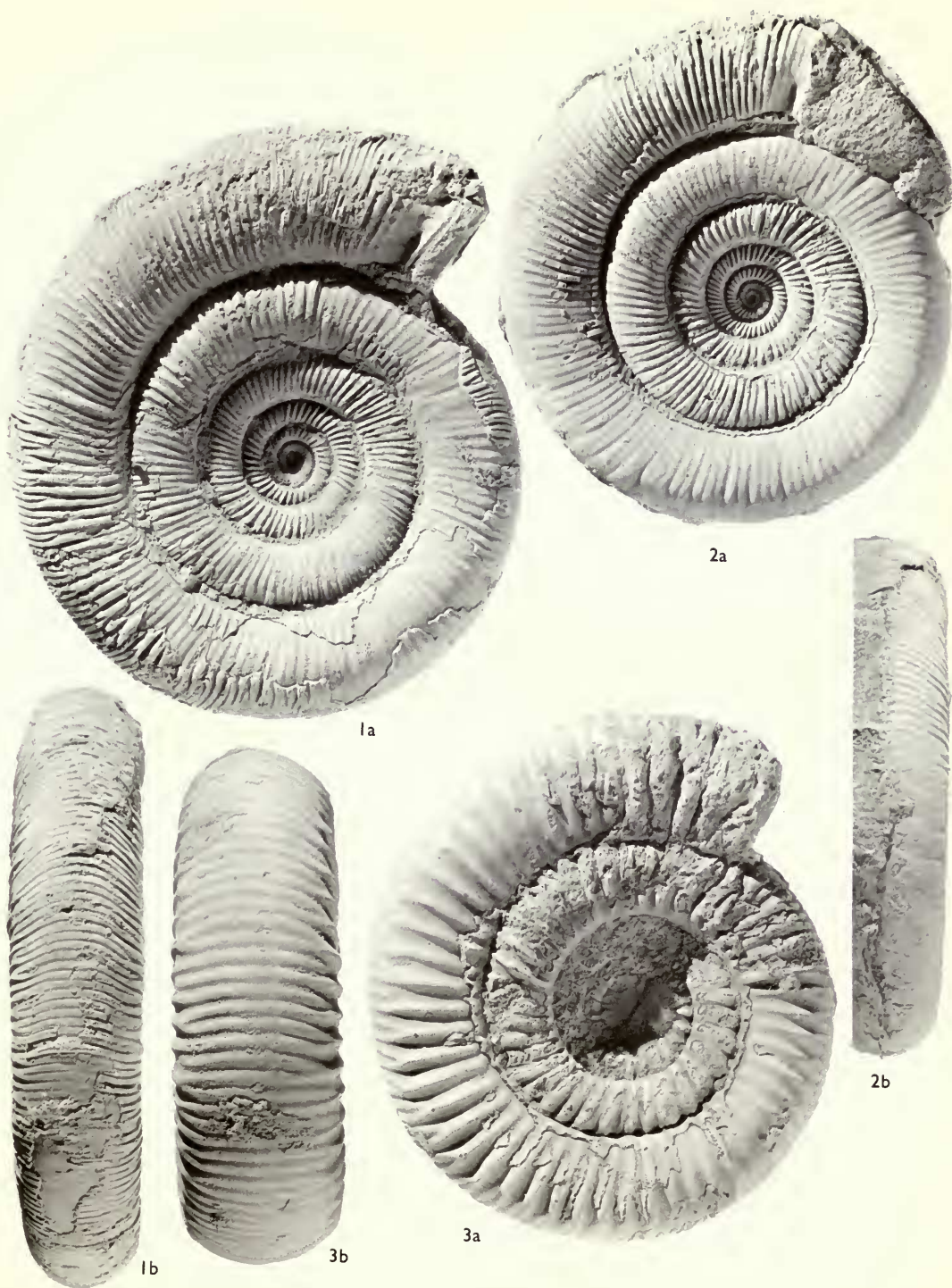


PLATE 6

Dactylioceras (Orthodactylites) semicelatum (Simpson)

FIG. 1. Grey Shales bed 28, Semicelatum Subzone, east Kettleness, C.77270.

Dactylioceras (Orthodactylites) tenuicostatum (Young & Bird)
Tenuicostatum Subzone.

FIG. 2. Grey Shales bed 24, west of Port Mulgrave, C.77237.

FIG. 3. Grey Shales bed 20, Holmsgrove Sand, C.77109.

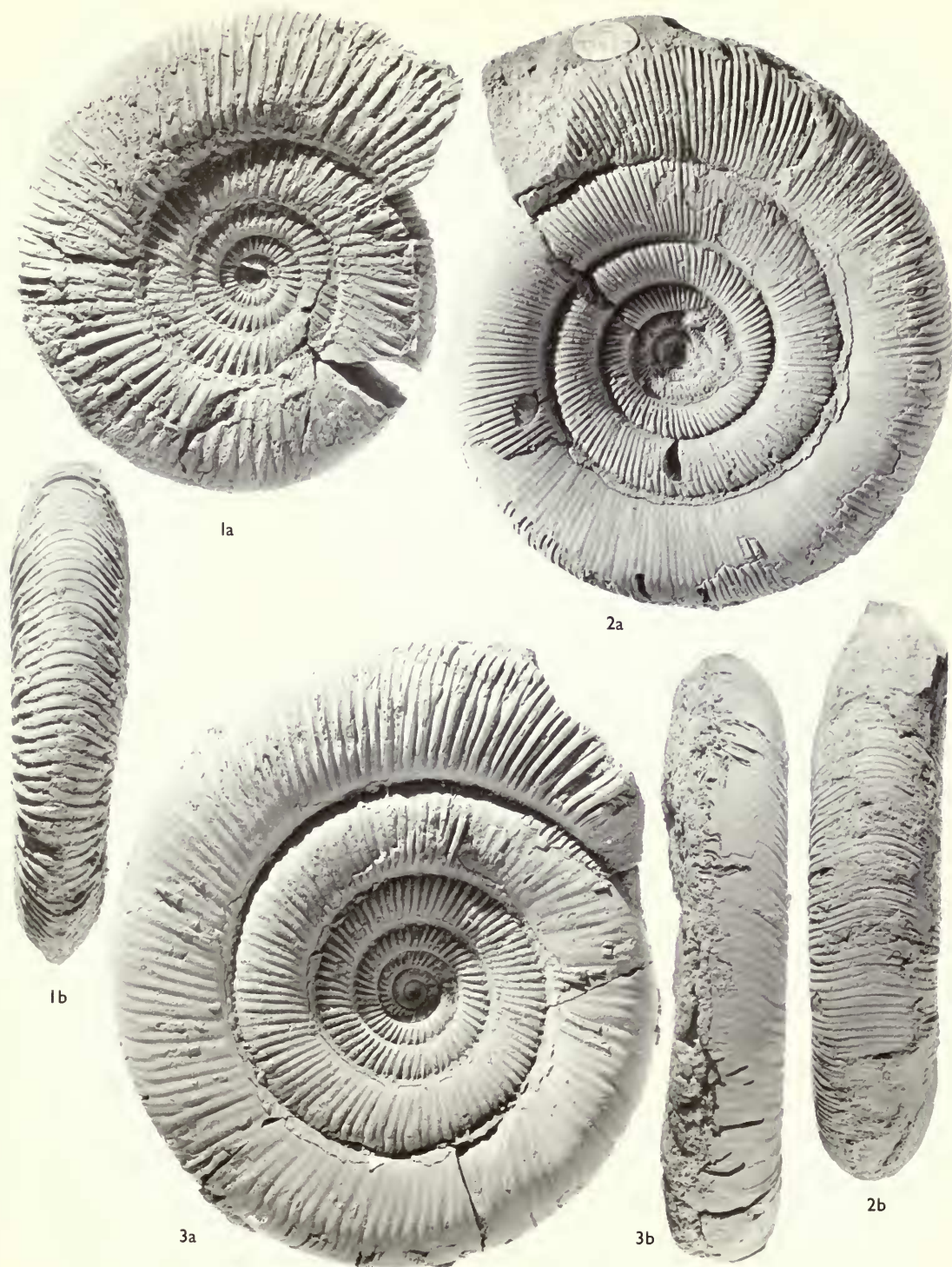


PLATE 7

Dactylioceras (Orthodactylites) semicelatum (Simpson)
Semicelatum Subzone.

FIG. 1. Grey Shales bed 30, Loop Wyke, C.77329.

FIG. 2. Grey Shales bed 28, west of Port Mulgrave, C.47940.

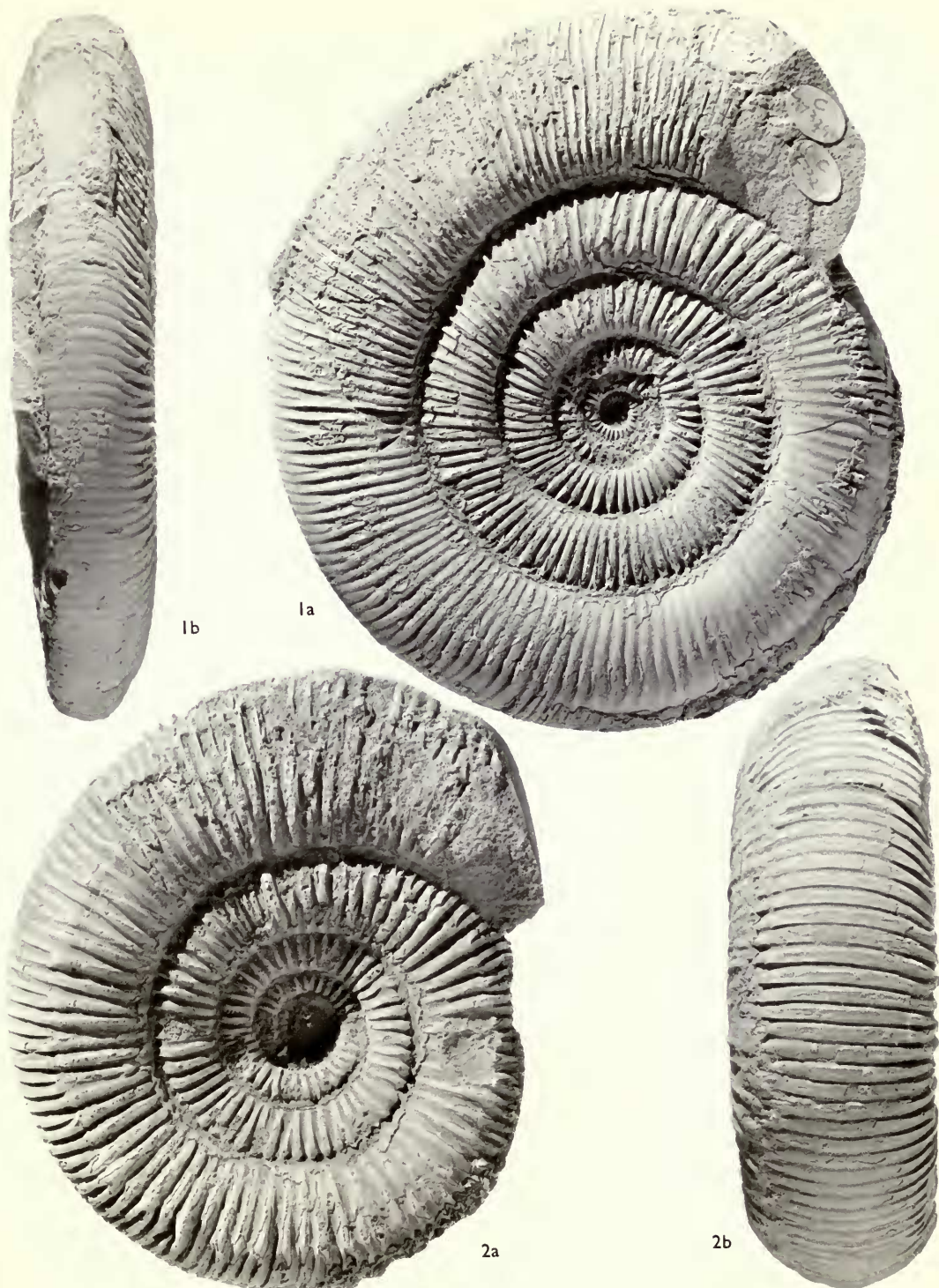


PLATE 8

Dactylioceras (Orthodactylites) semicelatum (Simpson)

Semicelatum Subzone.

FIGS. 1-3. Grey Shales bed 30, east Kettleness, C.77302, C.77305 and C.77314.

FIG. 4. Grey Shales bed 31, 1.22m (4ft) above the base, base of cliff south of Lingrow Knock, C.47932.

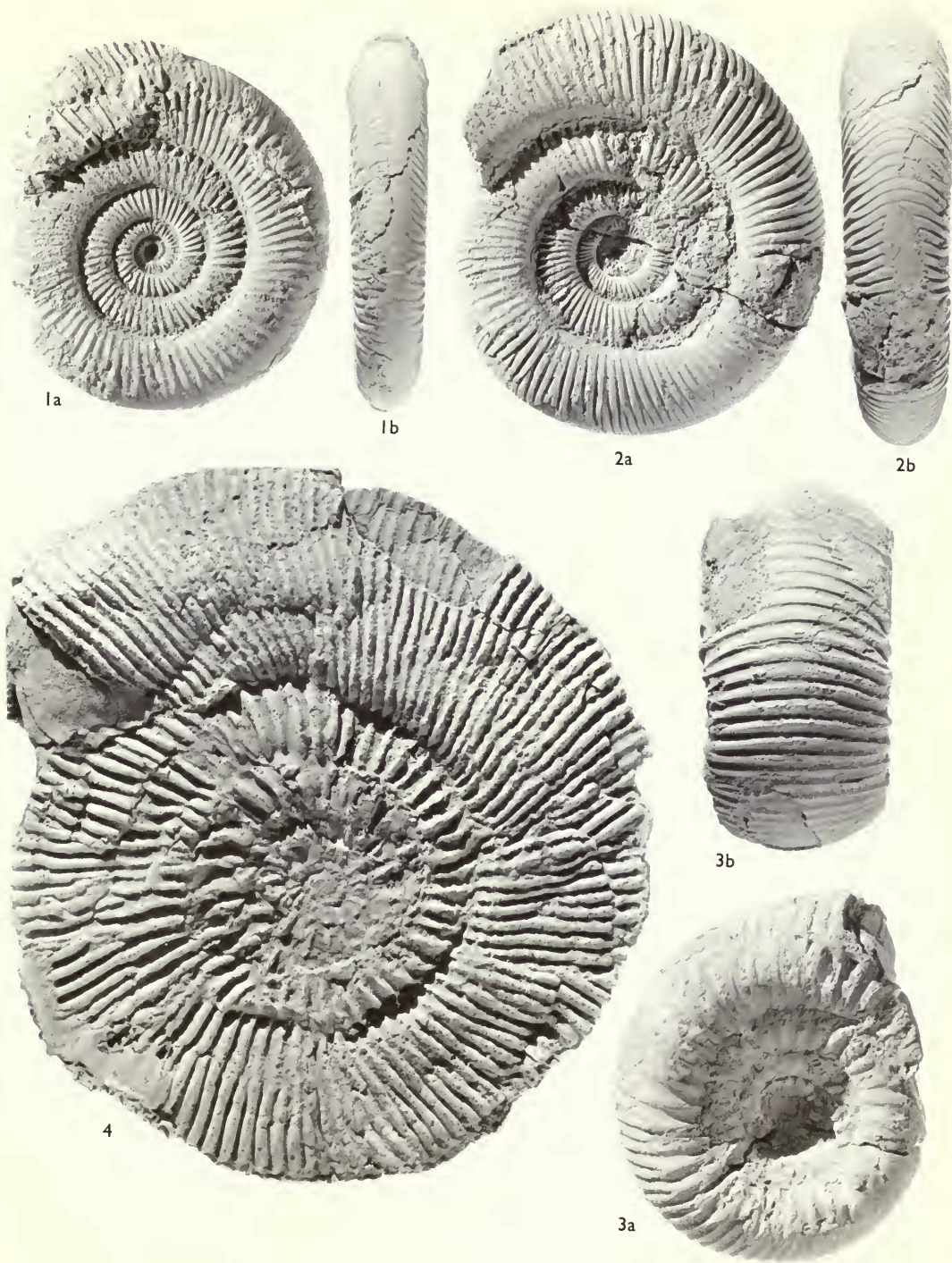


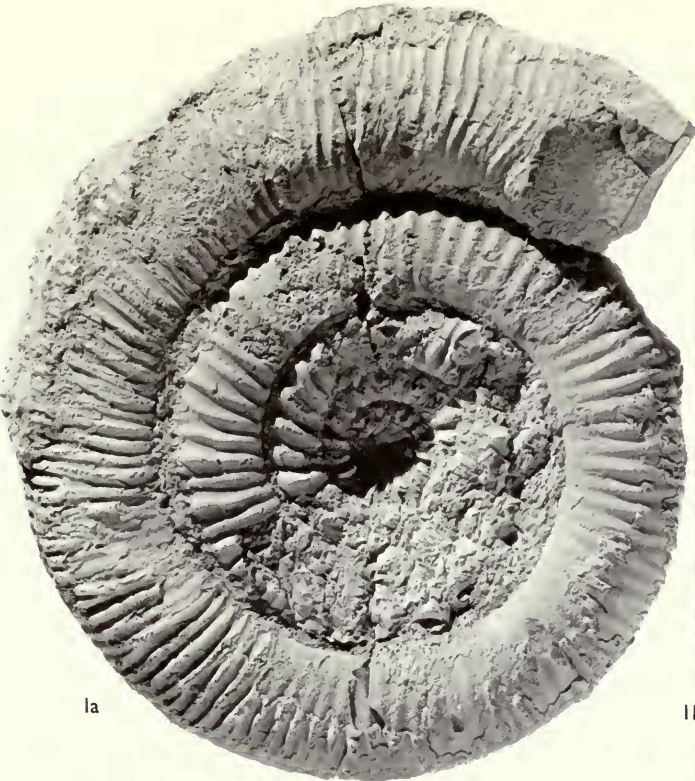
PLATE 9

Dactylioceras (Orthodactylites) semicelatum (Simpson)

Semicelatum Subzone.

FIGS. 1, 2. Grey Shales bed 30; Fig. 1. Hawsker Bottoms, C.77317; Fig. 2. West of Port Mulgrave, C.47956.

FIG. 3. With '*Posidonia*' *radiata* (Goldfuss), Grey Shales bed 32, shell bed at base, west of Port Mulgrave, C.77360.



1a

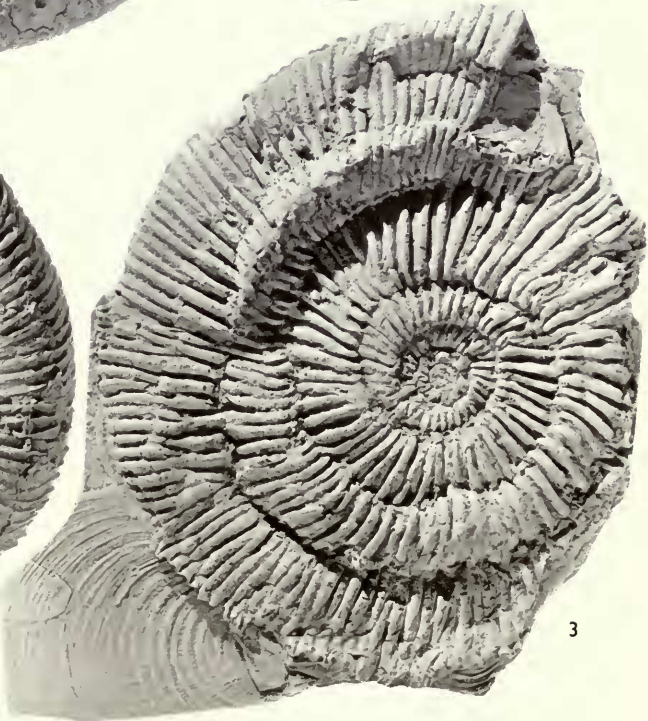


1b

2b



2a



3